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# EFFECT OF THE RELATIVE LENGTH OF DAY AND NIGHT AND OTHER FACTORS OF THE ENVIRONMENT ON GROWTH AND REPRODUCTION IN PLANTS

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## INTRODUCTION

The importance of the relationships existing between light and plant growth and development has been so long recognized and these relationships have been of so much interest to investigators that a very extensive literature on the subject has been developed. For present purposes it will not be necessary to attempt even a brief review of this literature, and only some of the leading features bearing upon the particular problems in hand need to be touched upon. For more extended discussions of the work in this field the monographs of MacDougal (*18*)[2] and Wiesner (*26*) may be consulted. Three primary factors enter into the action of light upon plants—namely, (1) the intensity of the light, (2) the quality, that is, the wave length of the radiation, and (3) the duration of the exposure. Most phases of these three factors have been more or less extensively investigated. In the present investigation we are concerned chiefly with the general growth and development of plants and the reproductive processes as affected by the daily duration of the light exposure.

As regards intensity, it seems to be pretty well established that there is an optimum for growth in each species and that for many species this optimum is less than the intensity of the full sunlight on a clear day. Within limits, reduction in light intensity tends to lengthen the main

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[2] Reference is made by number (italic) to "Literature cited," p. 605-606.

axis and branches and to increase the superficial area of the foliage of many species. Also, the thickness of the leaf lamina may be reduced, and there may be marked departures from the normal in internal structure, the tendency being toward a less compact structure. So far as is known, no important general relationships between differences in light intensity and reproductive processes have been experimentally demonstrated.

The comparative effects produced by different regions of the spectrum, including the ultra-violet, have been extensively investigated but with more or less conflicting results. The most extensive investigations on the subject, perhaps, have been made by Flammarion (*8*). It was found that there is abnormal elongation of the principal axis in several species under the influence of the red rays, while growth is markedly reduced under the green and especially under the blue rays. In some plants, however, such as corn, peas, and beans, growth is greatest in white light. Some plants blossomed considerably earlier in red light than in white. White light produced the greatest weight of dry matter. Leaves of Coleus developed decided differences in color patterns under differently colored lights. In subsequent work Flammarion has extended his studies to a large number of species.

The duration of the daily exposure to light needs to be considered in three separate phases—(1) continuous illumination throughout the 24-hour period, (2) continuous darkness throughout, leading to the phenomena of etiolation, and (3) illumination for any fractional portion of the 24-hour day. Under natural conditions continuous sunlight throughout the 24-hour period occurs, of course, only in very high latitudes. Schübeler (*23*) observed the behavior of several species transported from lower latitudes and grown in northern Scandinavia under continuous sunlight lasting for a period of two months. In the species under observation the vegetative period was shortened and the seeds produced were larger than the normal. It is stated, also, that there was an increased formation of aromatic and flavoring constituents. Another method of securing continuous illumination consists in the use of artificial light for illumination or in the supplementing of normal daylight with artificial light, though, of course, the quality and the intensity from the two sources will not ordinarily be the same. Using electric light alone, of an intensity one-third that of sunlight, Bonnier (*6*) observed a marked increase in chlorophyll formation which extended inwardly to unusual depths. He found also incomplete differentiation of the tissues, recalling, in this respect, the effects of continued darkness. In some instances the color of blossoms was deepened.

Etiolation, resulting from exposure to continuous darkness, has been the subject of much study. In this connection special mention should be made of the work of MacDougal (*18*) covering a very large number of species. This author also presents a comprehensive survey of previous

work on the subject. In most instances stems, and frequently leaves, exhibited negative geotropism in the absence of light. In all species investigated etiolated tissues show a lesser degree of differentiation than the normal. In this connection MacDougal points out that the differences exhibited between etiolated specimens and normal plants demonstrate the fact that growth, or increase in size, and development, or differentiation, are distinct processes capable of separation. For present purposes perhaps his most important observation is that in no plant investigated had the stamens and pistils attained functional maturity.

The effects of differences in the length of the daylight period, the subject of the present study, have not been so extensively investigated as most other phases of light action. Obviously the problem may be approached in any one of four ways: by comparing the behavior of plants when propagated in different latitudes, by growing plants at different seasons of the year in the same latitude, by supplementing the daylight period with artificial light, and by preventing light from reaching the plant for a portion of the normal daylight period. In the records of attempts to grow various plants in different parts of the world there are undoubtedly a great deal of available data bearing on the present problem; but apparently no systematic effort has been made to utilize this material, the reason probably being that the importance of the relative length of day in affecting plant processes, and, in particular, reproduction, has not been appreciated. Bailey (*3*, *4*, *5*,) carried out an extensive series of tests in which daylight illumination was supplemented by the electric arc light applied for different portions of the night. The addition of the artificial light induced blossoming and seed formation in spinach. The additional light also favored the growth of lettuce. Rane (*20*), using the incandescent filament electric light, and Corbett (*7*), employing incandescent gas light, observed that certain flowering plants and some vegetables blossomed somewhat earlier when the normal daylight illumination was supplemented with artificial light. In most of these tests the artificial light was applied for the entire night, but apparently the results so far as concerns reproduction were essentially the same as when the plants were darkened for a portion of the night. Tournois (*24*, *25*) has reported the results of an interesting experiment with hemp (*Cannabis sativa* L.) and a species of hops (*Humulus japonicus* Sieb. and Zucc.) in which these plants were exposed to sunlight only from 8 a. m. to 2 p. m. daily. It had been shown by Girou de Buzareingues (*10*) as early as 1831 that when planted in the late winter or very early spring months the hemp plant first develops in the spring a number of abnormal sterile blossoms in the leaf axils and later produces normal flowers at the regular blossoming period. Following up this fact Tournois concludes from the above-mentioned experiment that the abnormal

blossoming period is induced by the short length of day prevailing in the early spring months.

In a few words, previous work on light action clearly indicates that permanent exclusion of light effectually prevents completion of the blossoming and seed-forming processes, while in certain cases lengthening the normal daily period of illumination by the use of artificial light or by propagation in far northern latitudes hastens the approach of the blossoming period, and, in the case of two species, shortening the daily exposure to light induces the formation of precocious blossoms. That the relative length of the day is really a dominating factor in plant reproduction processes, as is demonstrated in the present paper, seems not to have been suspected by previous workers in this field.

## PRELIMINARY OBSERVATIONS

In 1906 there were observed in a strain of Maryland Narrowleaf tobacco (*Nicotiana tabacum*, L.), which is a very old variety, several plants which grew to an extraordinary height and produced an abnormally large number of leaves. As these plants showed no signs of blossoming with the advent of cold weather, some of them were transplanted from the field to the greenhouse and the stalks of others were cut off and the stumps replanted in the greenhouse. These roots soon developed new shoots which blossomed and produced seed, as did also the plants which had been transferred in their entirety. This very interesting giant tobacco, commonly known as Maryland Mammoth, which normally continues to grow till cold weather in the latitude of Washington, D. C., without blossoming, proved to be a very valuable new type for commercial purposes, but the above-mentioned procedure has been the only method by which seed could be obtained. The type bred true from the outset, and no matter how small the seed plant the progeny have always shown the giant type of growth when propagated under favorable summer conditions. It may be remarked at this point that inheritance of gigantism[1] in this tobacco has been studied by one of the present writers (*2*) and it has been shown that this character acts as a simple Mendelian recessive.

On one occasion it was observed that seedlings of the Mammoth transplanted to 8-inch pots in late winter blossomed in early spring after reaching a height of some 3 feet and developed an excellent crop of seed. From this it was at first concluded that growing the plant under conditions of partial starvation would induce blossoming, but this idea proved to be erroneous. Repeated attempts during the summer months to force blossoming by subjecting the plant to conditions which would permit only limited growth were futile. On the other hand, it was found that

[1] Throughout this paper the term gigantism is used to signify a tendency toward more or less indefinite vegetative activity manifested by plants under certain favorable environmental conditions. Though an inherited characteristic, it may come into expression only under definite conditions of environment; and the present investigation seems to make it clear that the length of the daily light exposure is the controlling factor.

seedlings grown in the greenhouse during the winter months invariably blossomed without regard to the size of the pot containing the seedling or the extent to which the plant was stunted by unfavorable nutrition conditions. The seedlings behaved, therefore, like the summer-grown giant plants which were transferred to the greenhouse late in the fall. Finally, it was observed that the shoots which were constantly developing from the transplanted roots of giant plants transferred to the greenhouse blossomed freely during the winter months, but as early spring advanced blossoming soon ceased and the younger shoots once more developed giant stalks. Obviously, then, the time of year in which the Mammoth tobacco develops determines whether the growth is of the giant character. During the summer months the plants may attain a height of 10 to 15 feet or more and produce many times the normal number of leaves without blossoming, while during the winter months blossoming invariably occurs before the plants attain a height of 5 feet. Naturally it became of interest from both a practical and a scientific standpoint to determine the factor of the environment responsible for the remarkable winter effect in forcing blossoming. It may be added just here that gigantism also has been observed in several distinct varieties of tobacco other than the Maryland—namely, in Sumatra, Cuban, and Connecticut Havana.

Again, in following out an investigation on the relation of the nutrition conditions to the quantity of oil formed in the seeds of such plants as cotton, peanuts, and soybeans, the present writers (*9*) had occasion to investigate the significance of the observation made by Mooers (*19*), that successive plantings of certain varieties of soybeans (*Soja max* (L.) Piper) made through the summer months, show a decided tendency to blossom at approximately the same date regardless of the date of planting. In other words, the later the planting the shorter is the period of growth up to the time of blossoming. In the course of the investigation on oil formation it became desirable to study the possible effects of temperature differences on the process. Since it is much simpler and cheaper to maintain temperature differences during the winter by the use of heat than during the summer by means of refrigeration, it was planned to make some tests with soybeans during the winter. It was soon found, however, that the plants began to develop blossoms before they had made anything like a normal growth, and the few blossoms produced were cleistogamous, so that it became necessary to abandon the plan of conducting the tests in question during the winter months. As is the case with the Mammoth tobacco, the time of year in which the plants are grown exerts a very profound influence on growth and reproduction in the soybean.

In seeking a solution of the problem as to why the behavior of these plants is radically different from the normal during the fall and winter months one naturally thinks of light and temperature as possible factors. It was observed, however, that both the Mammoth tobacco and the

soybeans still showed the abnormal behavior in the winter even when the temperature in the greenhouse was kept quite as high as prevails out of doors during the summer months. This observation seemed to dispose of temperature as a possible factor of importance in the "winter effect." It is clear that the quantity of solar radiation received by plants is less in winter than in summer, for both the number of hours of sunshine per day and the intensity of the light are reduced during the winter months. The quality of the light also is affected, since the angle of elevation of the sun's path during the winter is less than during the summer and the selective absorptive action of the atmosphere comes into play. It happened that in the investigation on oil formation in seeds a number of experiments had been made with soybeans to determine the effect of light intensity on this process and, incidentally, it was observed that in no case was the date of blossoming materially affected by the intensity of the light. It had been found, also, that partial shading was without decided effect on the blossoming of the Mammoth tobacco. In view of these experiences it hardly seemed likely that the other primary factor controlling the maximum amount of radiation received by the plant—namely, the length of the daily exposure—could be responsible for the effects in question. Nevertheless, the simple expedient of shortening artificially by a few hours the length of the daily exposure to the sun by use of a dark chamber was tried, and some very striking results were obtained, as detailed in the following paragraphs.

## PLAN OF THE EXPERIMENTS

The first experiments with the use of the dark chamber were begun in July, 1918. A small, ventilated, dark chamber with a door which could be tightly closed was placed in the field. The soybeans used in the tests were grown in wooden boxes 10 inches wide, 10 inches deep, and 3 feet long. These containers have been extensively used in growing soybeans and other small plants under controlled conditions, and it has been found that normal plants are easily obtained in this way. The dark chamber and the type of box used for growing soybeans and similar plants are shown in Plate 64, A. Larger plants like tobacco have been grown in large galvanized iron buckets or, in some cases, in ordinary flower pots. When the test plants have attained the desired stage of development the procedure has been to place them in the dark chamber at the selected hour in the afternoon each day. The plants were left in the dark chamber till the hour decided upon in the following morning, when they were again placed in the sunlight. This procedure was followed each day till the test was completed. Appropriate control plants were left in the open throughout the test in each case. By this method the number of hours of exposure to sunlight during the 24-hour period could be reduced as far as desired.

In the preliminary tests of 1918 no special means were provided for moving the boxes and pots containing the plants in and out of the dark chamber. In the spring of the present year a much larger dark house was constructed, and suitable facilities were installed for easily moving the test plants in or out of the house as often as desired. The dark house consisted of a rectangular frame structure 30 feet by 18 feet and 6 feet in height to the eaves and 9 feet to the ridgepole. All crevices by which light could enter were covered, tight-fitting doors were provided, and the interior was painted black. Means were provided at the bottom and top of the house for free circulation of air without the admission of light. A series of four steel tracks, each entering through a separate door, was provided; and on these tracks were mounted a number of trucks carrying the test plants in their containers. This equipment proved very satisfactory. A general view of the dark house, the trucks, and the test plants is shown in Plate 64, B.

It has been rather generally assumed that the pronounced changes in plant activities which come on with the approach of fall are due in some way to the lower mean daily temperatures or the wider daily range in temperature caused by cool nights. It seemed desirable, therefore, to compare the temperatures inside and outside the dark house, and for this purpose thermographs were installed. It was found that there were only slight differences in temperature. The temperature inside the dark house tended to run 2° or 3° F. higher than the temperature outside, particularly at night. Hence, any responses on the part of the plants resembling those appearing in the fall of the year could not be attributed to lower temperatures. To guard further against possible temperature effects, as soon as the above-mentioned temperature difference was discovered all doors of the dark house were opened as darkness came on each day.

In the various tests the length of the exposure to light was varied from a minimum of 5 hours per day to a maximum of 12 hours, 7 hours and 12 hours being the exposures chiefly used. For the shortest exposure the plants were placed in the dark house at 3 o'clock p. m. and returned to the light at 10 a. m.; for the 7-hour exposure the plants were darkened at 4 p. m. and returned to the light at 9 a. m.; and for the 12-hour exposure they were in the dark house from 6 p. m. till 6 a. m. A further modification in exposure consisted in placing the plants in the dark house at 10 a. m. and returning them to the light at 2 p. m. In most instances the daily treatment began with the germination of the seed or in the earlier stages of growth and continued until maturity, but in some cases the plants were permanently restored to the open as soon as blossoming occurred, and in other cases the artificial shortening of the day was not begun until after blossoming had occurred. To facilitate discussion it will be convenient to use the expressions "long day" as meaning exposure to light for more than 12 hours and "short day" as referring to an exposure of 12 hours or less. The term "length of day"

as used in this paper refers to the duration of the illumination period for each 24-hour interval.

As a part of the present investigation a series of plantings of soybeans was made in the field at intervals of approximately three days throughout the season, in order that the effects produced by different dates of planting might be compared with those produced by artificially shortening the length of the daily exposure to light.

## BEHAVIOR OF THE PLANTS TESTED

The initial experiment was made in the summer of 1918, and in this instance a box containing the Peking variety of soybeans in blossom and three pots containing Mammoth tobacco plants which had been growing for several weeks were first placed in the dark chamber at 4 p. m. on July 10 and removed therefrom at 9 a. m. the following morning. This treatment was continued each day till the seeds of the beans and tobacco were mature. All subsequent experiments were made during the year 1919. Details of the tests for both years follow.

### SOYBEANS (SOJA MAX (L.) PIPER)

(a) MANDARIN [1] (F. S. P. I. No. 36,653), early maturing:

(1) Exposed to light from 10 a. m. to 3 p. m. Planted May 8, up May 17, and placed in dark house May 20. First blossoms appeared June 12 on test plants and June 15 on controls. Average height of test plants 6 to 7 inches and that of controls 18 to 20 inches. After blossoming, the growth and development of the seed pods was much more rapid in the test plants than in the controls.

(2) Exposed to light from 9 a. m. to 4 p. m. Planted May 8, up May 17, and placed in dark house May 20. First blossoms appeared June 10 on test plants and June 15 on controls. Average height of test plants 9 to 10 inches and that of controls 19 to 20 inches.

(3) Exposed to light from 6 a. m. to 6 p. m. Planted and placed in dark house June 11, up June 16. First blossoms appeared July 7 on test plants and July 14 on controls. Average height of test plants 14 to 15 inches and that of controls 32 to 33 inches. Six weeks after blossoming the seed pods and foliage were still green and the plants stocky, whereas, under the same conditions, the Peking variety, listed below, showed many brown, mature pods, foliage yellowing, and the plants slender.

(b) PEKING [1] (F. S. P. I. No. 32,907), medium maturing:

(1) Exposed to light from 10 a. m. to 3 p. m. Planted May 8, up May 17, and placed in dark house May 20. First blossoms appeared June 12 on test plants and July 21 on controls. Seed pods on test plants

[1] Horticultural variety.

were turning brown by July 18, and all were mature before August 10. Average height of test plants 5 to 6 inches and that of controls 42 to 43 inches. Test plants were restored to normal light exposure June 20.

(2) Exposed to light from 9 a. m. to 4 p. m. Planted May 8, up May 17, and placed in dark house May 20. First blossoms appeared June 10 on test plants and July 21 on controls. Average height of test plants 8 inches and that of controls 45 to 48 inches. See Plate 65.

(2a) Exposed to light from 9 a. m. to 4 p. m. Planted May 8, up May 17, placed in dark house June 7. First blossoms June 29. Average height of plants 16 to 17 inches.

(3) Exposed to light from 9 a. m. to 4 p. m. after blossoming. Planted May 7, blossomed July 9, and first placed in dark house July 10. By July 26 there were many full-grown pods on test plants while there were none on controls more than half-grown. By August 29 the leaves had yellowed and were falling, and some pods were fully ripe on test plants while control plants were still green. By September 7 all seeds were fully ripe on test plants, but those on controls did not fully mature till about October 1. See Plate 66.

(4) Exposed to light from 6 a. m. to 6 p. m. Planted and placed in dark house June 11, up June 16. First blossoms July 7 on test plants and August 6 on controls. Average height of test plants 14 to 15 inches and that of controls 39 to 40 inches.

(5) Exposed to light from daylight to 10 a. m. and from 2 p. m. till dark. Planted June 14, up June 19, and placed in dark house June 19. First blossoms July 29 on test plants and August 11 on controls. Average height of test plants 25 to 26 inches and that of controls 41 to 42 inches.

(c) TOKYO,[1] late maturing:

(1) Exposed to light from 10 a. m. to 3 p. m. Planted May 8, up May 17, and placed in dark house May 20. First blossoms appeared June 13 on test plants and July 29 on controls. Average height of test plants 7 to 8 inches and that of controls 49 to 50 inches. Test plants were restored to normal light exposure June 20.

(2) Exposed to light from 9 a. m. to 4 p. m. Planted May 8, up May 17, and placed in dark house May 20. First blossoms appeared June 13 on test plants and July 29 on controls. Average height of test plants 7 to 8 inches and that of controls 49 to 50 inches.

(2a) Exposed to light from 9 a. m. to 4 p. m. Planted May 8, up May 17, and placed in dark house June 7. First blossoms appeared July 4. Average height of plants 23 to 24 inches.

(3) Exposed to light from 6 a. m. to 6 p. m. Planted and placed in dark house June 11, up June 16. First blossoms appeared July 14 on test plants and August 21 on controls. Average height of test plants 17 to 18 inches and that of controls 42 to 43 inches.

[1] Horticultural variety.

(4) Exposed to light from daylight till 10 a. m. and from 2 p. m. to darkness. Planted June 14, placed in dark house June 16, up June 19. First blossoms appeared August 20 on test plants and August 23 on controls. Average height of test plants 24 to 25 inches and that of controls 42 to 43 inches.

(d) BILOXI,[1] very late maturing:

(1) Exposed to light from 10 a. m. to 3 p. m. Planted May 8, up May 17, and placed in dark house May 20. First blossoms appeared June 16 on test plants and September 4 on controls. Average height of test plants 6 to 7 inches and that of controls 57 to 58 inches. See Plate 68, A. Test plants were restored to normal light exposure June 20.

(2) Exposed to light from 9 a. m. to 4 p. m. Planted May 8, up May 17, and placed in dark house May 20. First blossoms appeared June 15 on test plants and September 4 on controls. Average height of test plants 11 inches and that of controls 57 to 58 inches. See Plate 67.

(2a) Exposed to light from 9 a. m. to 4 p. m. Planted June 10, up June 15, and placed in dark house June 24. First blossoms July 22 on test plants and September 15 on controls. Average height of test plants 15 to 16 inches and that of controls 56 to 58 inches.

(3) Exposed to light from 6 a. m. to 6 p. m. Planted and placed in dark house June 11, up June 16. First blossoms appeared July 14 on test plants and September 8 on controls. Average height of test plants 23 to 24 inches and that of controls 54 to 55 inches. See Plate 68, B.

(4) Exposed to light from daylight to 10 a. m. and from 2 p. m. to darkness. Planted June 14, placed in dark house June 16, up June 19. First blossoms appeared September 6 on test plants and September 15 on controls. See Plate 69, A. Average height of test plants 39 to 40 inches and that of controls 47 to 48 inches. In all of the above-described tests with soybeans observations were made on from 20 to 25 individuals.

## TOBACCO (NICOTIANA TABACUM AND N. RUSTICA L.)

(a) NICOTIANA TABACUM;[1] MARYLAND MAMMOTH, giant type:

(1) Exposed to light from 10 a. m. to 3 p. m. Observations on 14 test plants and 10 controls. Planted March 6, transplanted to 6-inch pots May 10, and placed in dark house May 14. First blossoms appeared July 8 to August 14 on test plants and in last week of October on controls. Average height of test plants 14 to 16 inches and that of controls 3 to 5 inches.

(2) Exposed to light from 9 a. m. to 4 p. m. Observations on 7 test plants and 10 controls. Planted March 6, transplanted to 6-inch pots May 10, and placed in dark house May 14. First blossoms appeared July 18 to August 1 on test plants and in last week of October on controls.

[1] Horticultural variety.

Average height of test plants 12 to 14 inches and that of controls 5 to 6 inches.

(2a) Exposed to light from 9 a. m. to 4 p. m. Observations on 8 test plants and 8 controls. Planted January 8, transplanted to 8-inch pots May 3, and placed in dark house May 14. First blossoms appeared July 5 to 25 on test plants and October 1 to 25 on controls. See Plate 70.

(2b) Exposed to light from 9 a. m. to 4 p. m. Obseravtions on three test plants and four controls. Planted April 14, transplanted in steam-sterilized soil in 12-quart iron pails and placed in dark house June 10. First blossoms appeared August 1 to 7 on test plants and August 30 to September 8 on controls. Average height of test plants 37 inches and that of controls 39 inches.

(3) Exposed to light from 6 a. m. to 6 p. m. Observations on 6 test plants and 3 controls. Planted April 14 and transplanted to 12-quart iron pails containing steam-sterilized soil and placed in dark house June 11. First blossoms appeared August 26 to September 4 on test plants and September 3 to 20 on controls. Average height of test plants 48 inches and that of controls 49 inches. See Plates 71 and 72, A.

(b) N. TABACUM; STEWART 70-LEAF CUBAN,[1] giant type:

(1) Exposed to light from 9 a. m. to 4 p. m. Observations on 6 test plants and 5 controls. Planted April 14 and transplanted in steam-sterilized soil in 12-quart iron pails and placed in dark house June 10. First blossoms appeared August 16 to September 2 on test plants and September 24 to October 10 on controls. Average height of test plants 53 to 69 inches and that of controls 73 to 84 inches.

(c) N. TABACUM; CONNECTICUT BROADLEAF:[1]

(1) Exposed to light from 9 a. m. to 4 p. m. Observations on 11 test plants and 10 controls. Planted April 14 and transplanted to 14-quart iron pails and placed in dark house June 5. First blossoms appeared July 18 to 24 on test plants and July 17 to 22 on controls. Average height of test plants 38 inches and that of controls 34 inches. Average number of nodes on test plants 36 and same number on controls.

(1a) Exposed to light from 9 a. m. to 4 p. m. Observations on 8 test plants and 6 controls. Planted April 5 and transplanted to 14-quart iron pails and placed in dark house May 28. First blossoms appeared July 13 to 20 on test plants and July 7 to 15 on controls. Average height of test plants 37 inches and that of controls 40 inches.

(d) N. RUSTICA:

(1) Exposed to light from 9 a. m. to 4 p. m. Observations on 5 test plants and 3 controls. Planted April 14, transplanted to 14-quart iron pails, and 5 plants placed in dark house on June 2. Test plants blossomed July 5 to 28 and controls July 1 to 12.

[1] Horticultural variety.

ASTER LINARIIFOLIUS L.

A common wild aster found in dry, open situations from Maine to Wisconsin and southward. The normal blossoming period begins about September 1 and extends over a period of two or three months.

(1) Exposed to light from 9 a. m. to 4 p. m. Six individuals taken from the field May 13 and transplanted to boxes of the type used for soybeans, three plants to the box. One box of the plants placed at once in the dark house. The control plants soon resumed vegetative development, throwing out numerous axillary branches on the upper portion of the stems as the normal limit in height was approached, thus following the regular course of development in the field. The test plants, on the other hand, made little additional growth and by June 1 were showing tiny flower heads. First blossoms appeared June 18 on test plants and September 12 on controls. Average height of test plants on June 24, 8 to 10 inches and that of controls 14 to 18 inches. Test plants were permanently returned to normal light on June 20. See Plate 72, B.

(2) Exposed to light from 6 a. m. to 6 p. m. Three individuals transplanted from field to each of two 8-gallon iron cans June 10 and those in one can placed in dark house June 12. Tiny flower heads were showing on the test plants by July 2. First blossoms appeared July 19 on test plants and September 20 on controls. Average height of test plants 8 to 9 inches and that of controls 14 to 15 inches.

(3) Exposed to light from daylight to 10 a. m. and from 2 p. m. to darkness. Three individuals transplanted from the field to each of two 8-gallon iron cans on June 14 and those in one can placed in dark house June 16. Flower heads were showing on both test plants and controls by August 20. First blossoms appeared September 16 on test plants and September 18 on controls. Average height of test plants 11 to 12 inches and that of controls 14 to 15 inches.

CLIMBING HEMPWEED (MIKANIA SCANDENS, L.)

A climbing composite, ranging from southern Maine to Florida and westward to Ontario, Mississippi, and Texas. The normal blooming period extends from late July to the latter part of September. The aerial summer growth perishes in the fall, and the plants are carried over the winter period by perennial underground shoots.

(1) Exposed to light from 9 a. m. to 4 p. m. A number of roots were transplanted from the field to 6-inch pots and placed in the greenhouse in November, 1918. These roots threw up shoots which made considerable growth during the winter months but did not blossom. On June 3 one plant was transferred to each of six 12-quart iron pails, three of which were placed in the dark house at once. The controls began blossoming in late July and continued to blossom profusely till the latter part of September. Some of the plants which had been left in the green-

house, where the temperature was much higher than out-of-doors, blossomed at the same time. The test plants behaved quite differently, for blossoming was completely inhibited throughout the summer. Moreover, the growth of the controls has been considerably greater than that of the test plants. See Plate 74.

BEANS (PHASEOLUS VULGARIS L.)

Three lots of seed of a tropical bean—two of which came from Arequipa, Peru, and one from Oruro, Bolivia—were planted together in two boxes measuring 3 feet by 10 inches by 10 inches on June 16, and one box was placed in the dark house June 24. Exposed to light from 9 a. m. to 4 p. m. According to Dr. D. N. Shoemaker this bean when planted in the field at Washington has been found to make a very large growth without blossoming till late in the fall, but when propagated in the greenhouse in the winter months the plant promptly blossoms and sets seed. The test plants blossomed July 21 to 23, and some of the seed pods were mature by August 22, whereas the controls did not blossom till October 11. The average height of the test plants was 4½ to 5 feet and that of the controls 7 to 8 feet. See Plate 73.

RAGWEED (AMBROSIA ARTEMISIIFOLIA L.)

Exposed to light from 9 a. m. to 4 p. m. Observations based on 6 test plants and 6 controls. Small plants taken from the roadside were transplanted to 6-inch pots on June 3, and a portion of these were immediately placed in the dark house. Staminate heads were showing on the test plants by June 17, and the anthers were shedding pollen freely by July 1. The controls did not begin blossoming till the last week in August, which is the normal period for the appearance of first blossoms on the plant. The average height of the test plants at the time of blossoming was 8 to 9 inches, while that of the controls on the same date was 11 inches and their final height 29 inches. The test plants were returned permanently to normal light exposure on July 1. See Plate 75, A.

RADISH (RAPHANUS SATIVUS L.)

SCARLET GLOBE:[1]

Exposed to light from 9 a. m. to 4 p. m. Planted May 15, up May 19, and placed in dark house on day of planting. The test plants grew more slowly than the controls for a time and then appeared to grow no further. All but two of the test plants, of which there were a large number, became diseased and finally died without forming seed stalks. The two survivors developed a crown of large leaves, and the roots also reached much larger proportions than those of the controls. Apparently enlargement of the roots had not ceased as late as October 15, when one

[1] Horticultural variety.

of them measured nearly 4 inches in diameter while its rosette of leaves measured 30 inches from tip to tip. Flower stems did not develop. The controls grew more rapidly from the outset, and all except three or four to be considered later formed flower stems in June, the first blossom appearing June 21. See Plate 75, B.

CARROT (DAUCUS CAROTA L.)

OXHEART:[1]

Exposed to light from 9 a. m. to 4 p. m. Planted June 4 and at once placed in dark house. The test plants made a uniform but slow growth, and the roots, which were very small, appeared to be devoid of the yellow pigment, carotin, since they were almost snow-white in color. The controls grew and developed normally, the roots showing the normal yellow color. On August 19 the average height of the test plants was 8 to 9 inches and that of the controls 18 to 20 inches. See Plate 79, B.

LETTUCE (LACTUCA SATIVA L.)

BLACK SEEDED SUMMER:[1]

Exposed to light from 9 a. m. to 4 p. m. Planted in dark house June 4. Germination was satisfactory, but the seedlings made very little growth, and after a time all died. The controls grew vigorously but under the stimulus of the long day the plants soon sent up flowering shoots and blossomed.

HIBISCUS MOSCHEUTOS L.

A wild perennial in marshes, ranging from Ontario to Florida and Texas. Normal blooming period July to September. Exposed to light from 9 a. m. to 4 p. m. Planted in November in greenhouse. Seed did not germinate till the following March. Seven plants transferred to 12-quart iron pails on June 6, three of which were placed in dark house June 7. The test plants did not blossom nor did they make any growth during the summer. The controls grew vigorously, and the first blossoms appeared August 22 to September 10. The average height of the test plants was 12 inches and that of the controls 29 inches.

CABBAGE (BRASSICA OLERACEA CAPITATA L.)

EARLY JERSEY WAKEFIELD:[1]

Exposed to light from 9 a. m. to 4 p. m. Observations based on four test plants and four controls. Transplanted and placed in dark house on June 7. The test plants grew slowly but uninterruptedly throughout the season, although they showed little tendency to form heads. The control plants grew normally and formed large heads which eventually burst open, followed by the formation of new heads of small size.

[1] Horticultural variety.

VIOLETS (VIOLA FIMBRIATULA SM.)

A common wild species ranging from Nova Scotia to Wisconsin and southward and growing in sandy fields and on dry hillsides. The normal blooming period comes in April. Exposed to light from 9 a. m. to 4 p. m. Two lots of six plants were transferred from the field to two boxes measuring 3 feet by 10 inches by 10 inches on June 9, and one of the boxes was placed at once in the dark house. The test plants showed flower buds as early as June 21 and were in blossom early in July, producing purple, petaliferous flowers and also cleistogamous flowers. The control plants produced numerous cleistogamous flowers but none of the purple, petaliferous type.

EARLY GOLDENROD (SOLIDAGO JUNCEA AIT.)

The earliest species of goldenrod, ranging from New Brunswick to Saskatchewan and south to North Carolina and Missouri. Blossoming normally extends from late June to September. Exposed to light from 9 a. m. to 4 p. m. Two lots of six plants were transplanted to two boxes measuring 3 feet by 10 inches by 10 inches on June 6, and one of the boxes was at once placed in the dark house. The test plants and the controls blossomed at the same time, late in August. The test plants however, were shorter and more compact than the controls. The heights of the test plants averaged 24 inches and those of the controls 38 inches. The test plants advanced toward maturation more rapidly than the controls after the flowering stage had been reached.

EFFECT OF RESTORING THE TEST PLANTS TO NORMAL LIGHT EXPOSURE AFTER BLOSSOMING HAD OCCURRED

In the experiments with soybeans, aster, and ragweed described above it has been made clear that after blossoming has occurred the effect of shortening the daily exposure to sunlight is to hasten greatly the ripening of the seed. In certain instances, however, as has been recorded under the several experiments, the test plants were restored to the normal light exposure as soon as blossoming had occurred.

Under these conditions seed pods of the soybeans ripened rapidly, the leaves turned yellow, and for a time it appeared that the plants would die as is normal for the soybean. Eventually, however, new branches developed under the influence of the long summer days. The renewed growth was especially well-developedin the Biloxi variety, and the final result was that these plants, still bearing the first crop of ripened seed pods, blossomed for the second time September 4 to 8. This date of blossoming, moreover, is also that for the first blossoming of the control plants which had been planted on the same date as the test plants and had been exposed to the normal daylight period throughout their development.

Like the soybeans, the asters after a time responded to the long-day influence; and by July 20 the plants, though bearing ripened seed, were

developing new axillary branches. The new growth finally developed flower heads; and thus the plants blossomed for the second time during the first half of September, which is the time of blossoming of the original

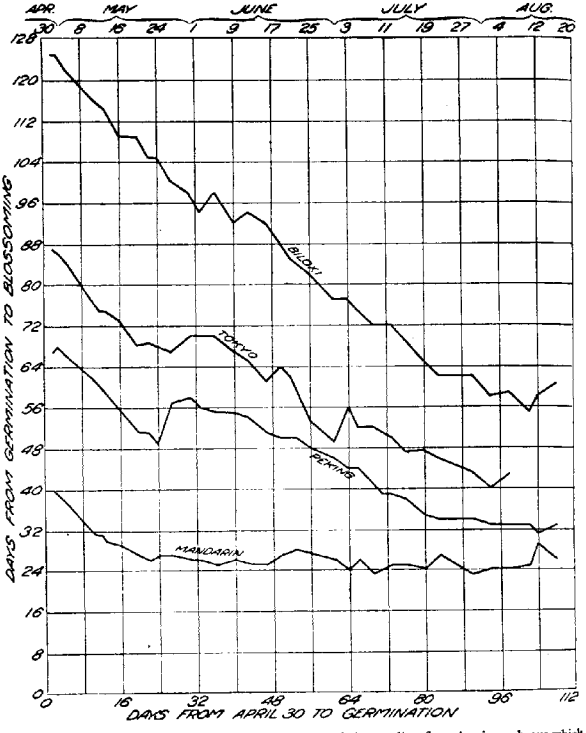



FIG. 1.—Graph showing the shortening of the vegetative period preceding flowering in soybeans which results from progressively later planting during the growing season.

controls exposed to the normal daylight period throughout their development.

The ragweed, likewise, resumed vegetative development after a time, and, in fact, under the influence of the full length of the daylight period the new growth exceeded in size that of the original plants. The plants blossomed the second time during the last week in August, which is also the time of blossoming of the original controls and of ragweed growing in the field. It may be noted, however, that while the original growth produced staminate spikes as well as pistillate flowers in the usual man-

ner, the second growth produced pistillate flowers almost exclusively and the leaves were mostly atypical.

## RELATION OF DATE OF PLANTING TO DATE OF BLOSSOMING IN SOYBEANS

Through the spring and summer of 1919 a series of plantings of soybeans which included the four varieties used in the tests described above were made in the field at regular intervals of three days as nearly as conditions would permit. All plantings of each variety consisted of rows 10 feet in length. The date recorded as that when first blossoms appeared is in each case that when the majority of the individuals in the planting first showed one or two open blossoms. In most instances the

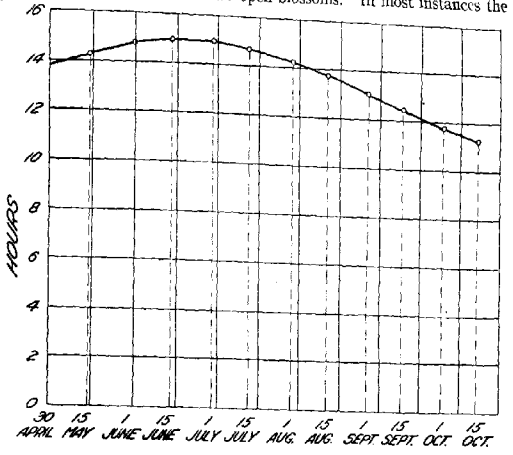



FIG. 2.—Graph showing changes in length of day during the growing season in the latitude of Washington, D. C. Ordinates indicate 2-hour intervals of the day and abscissae indicate 16-day periods of the growing season.

greater number of the individuals in a planting showed their first open blossoms on practically the same date. The dates of planting, germination, and appearance of first blossoms, together with the number of days from germination till blossoming are shown in Table I.

The effect of the date of planting on the length of the period from germination to the blossoming stage for each variety is more easily seen in the curves of figure 1, in the construction of which the number of days from April 30 to dates of germination are used as ordinates and the number of days included in the periods of growth prior to blossoming are used as abscissae. The relative length of the day—that is, the time between sunrise and sunset, expressed in 2-hour periods—also is shown for the same period in figure 2. The relative heights of the plants in the consecutive plantings of the Biloxi variety are shown graphically in figure 3.

TABLE I.—*Effect of date of planting on date of blossoming of soybeans grown in field at Arlington, Va., 1919*

| Date of planting. | Date of appearance above ground. | Mandarin. | | Peking. | | Tokyo. | | Biloxi. | |
|---|---|---|---|---|---|---|---|---|---|
| | | Date of first blossoms. | Time from germination to blossoming. | Date of first blossoms. | Time from germination to blossoming. | Date of first blossoms. | Time from germination to blossoming. | Date of first blossoms. | Time from germination to blossoming. |
| | | | *Days.* | | *Days.* | | *Days.* | | *Days.* |
| Apr. 9 | May 2 | June 11 | 40 | July 8 | 67 | July 28 | 87 | Sept. 4 | 125 |
| 14 | 3 | 11 | 39 | 10 | 68 | 28 | 86 | 5 | 125 |
| 18 | 5 | 11 | 37 | 10 | 66 | 28 | 84 | 4 | 122 |
| 22 | 10 | 11 | 32 | 11 | 62 | 26 | 77 | 4 | 117 |
| 26 | 11 | 11 | 31 | 11 | 61 | 26 | 76 | 4 | 116 |
| 30 | 12 | 12 | 31 | 11 | 60 | 26 | 75 | 4 | 115 |
| May 3 | 13 | 12 | 30 | 11 | 59 | 27 | 75 | 4 | 114 |
| 6 | 15 | 14 | 29 | 11 | 56 | 28 | 73 | 2 | 109 |
| 9 | 20 | 16 | 27 | 11 | 51 | 27 | 68 | 6 | 109 |
| 13 | 22 | 17 | 26 | 12 | 52 | 30 | 69 | 4 | 105 |
| 16 | 24 | 20 | 27 | 12 | 49 | 31 | 68 | 6 | 105 |
| 20 | 27 | 23 | 27 | 23 | 57 | Aug. 2 | 67 | 4 | 100 |
| 24 | 31 | 26 | 26 | 28 | 58 | 9 | 70 | 6 | 98 |
| 27 | June 2 | 28 | 26 | 28 | 56 | 11 | 70 | 4 | 94 |
| 31 | 5 | 30 | 25 | 30 | 55 | 14 | 70 | 11 | 98 |
| June 4 | 9 | July 5 | 26 | Aug. 3 | 55 | 15 | 67 | 11 | 92 |
| 7 | 12 | 7 | 25 | 5 | 54 | 16 | 65 | 20 | 94 |
| 11 | 16 | 11 | 25 | 6 | 51 | 16 | 61 | 11 | 92 |
| 14 | 19 | 16 | 27 | 8 | 50 | 22 | 64 | 15 | 88 |
| 17 | 22 | 20 | 28 | 11 | 50 | 23 | 62 | 15 | 85 |
| 20 | 25 | 22 | 27 | 12 | 48 | 17 | 53 | 15 | 82 |
| 23 | 30 | 26 | 26 | 15 | 46 | 18 | 49 | 15 | 77 |
| 26 | July 3 | 27 | 24 | 16 | 44 | 26 | 56 | 18 | 77 |
| 30 | 5 | 31 | 26 | 18 | 44 | 26 | 52 | 18 | 75 |
| July 3 | 8 | 31 | 23 | 18 | 41 | 29 | 52 | 18 | 72 |
| 7 | 12 | Aug. 6 | 25 | 20 | 39 | 31 | 50 | 22 | 72 |
| 10 | 15 | 9 | 25 | 22 | 38 | 31 | 47 | 22 | 69 |
| 14 | 19 | 12 | 24 | 23 | 35 | Sept. 4 | 47 | 20 | 63 |
| 17 | 22 | 18 | 27 | 25 | 34 | 6 | 46 | 22 | 62 |
| 25 | 29 | 21 | 23 | Sept. 6 | 39 | 10 | 43 | 29 | 62 |
| 29 | Aug. 2 | 26 | 24 | 6 | 35 | 11 | 40 | 29 | 58 |
| Aug. 2 | 6 | 30 | 24 | 8 | 33 | ..... | ..... | Oct. 4 | 59 |
| 5 | 10 | Sept. 4 | 25 | 11 | 33 | ..... | ..... | 4 | 55 |
| 8 | 12 | 10 | 29 | 12 | 31 | ..... | ..... | 9 | 58 |
| 11 | 16 | 11 | 26 | 18 | 33 | ..... | ..... | 16 | 61 |
| 14 | 17 | ..... | ..... | 19 | 33 | ..... | ..... | ..... | ..... |
| 20 | 25 | ..... | ..... | 26 | 31 | ..... | ..... | ..... | ..... |

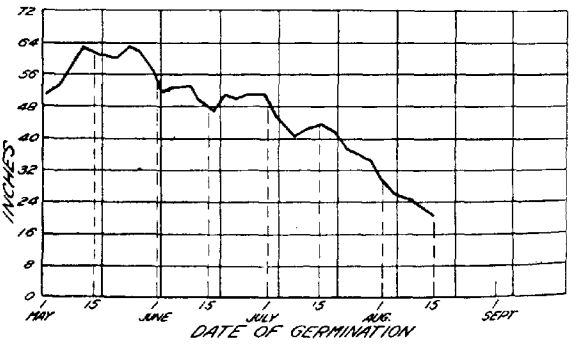



FIG. 3.—Graph showing the progressive decrease in height attained by Biloxi soybeans as the date of planting is delayed beyond late spring

## DISCUSSION OF RESULTS

The results of the experiments which have been described show clearly that both the rate and extent of the growth attained by the plants under study and the time required for reaching and completing the flowering and fruiting stages are profoundly affected by the length of the daily exposure to sunlight. The behavior of some of the plants under the different exposures would seem to indicate that the action on the vegetative phase of development is more or less independent of that on reproduction, but only tentative conclusions can be drawn on these points at the present time. The effects of the different light exposures on these two phases of plant development can best be discussed separately.

### LENGTH OF DAILY LIGHT EXPOSURE IN RELATION TO VEGETATIVE DEVELOPMENT

Under the conditions of the tests it was not possible to secure quantitative data on the various details of vegetative growth and development, but measurements of height and the photographic records will clearly indicate some of the differences resulting from the various light exposures. In general, the extent of growth was proportional to the length of the daily exposure to light; and this held true when the plants received two daily exposures to light, with an intervening period of darkening, as well as when there was only a single daily exposure to the light. Under the shorter exposures the plants were shorter and less stocky, and there were some indications of etiolation or chlorosis. Histological examination of the test plants was not undertaken, but in most species no very striking differences in gross anatomy resulted from the different exposures. Broadly speaking, the extent rather than the character of growth and vegetative development was chiefly affected. Table II is intended to bring out the relationship between size of plant and length of the exposure to the light for soybeans and the aster. This relationship is strikingly brought out for the Biloxi soybean in figure 3, which shows the decreasing heights of progressively later plantings. How length of exposure affects the Mandarin is shown in the foreground of Plate 78, B.

TABLE II.—*Effect of length of daily exposure to light on the height of soybeans and aster*

| Length of daily exposure. | Average heights of plants. | | | | |
|---|---|---|---|---|---|
| | Soybeans. | | | | Aster. |
| | Mandarin. | Peking. | Tokyo. | Biloxi. | |
| | *Inches.* | *Inches.* | *Inches.* | *Inches.* | *Inches.* |
| 10 a. m. to 3 p. m., 5 hours | 6 to 7 | 5 to 6 | 7 to 8 | 6 to 7 | ..... |
| 9 a. m. to 4 p. m., 7 hours | 9 to 10 | 8 | 7 to 8 | 11 | 8 to 10 |
| Daylight to 10 a. m. and 2 p. m. till dark, 8¼ to 11 hours[a] | ..... | 25 to 26 | 24 to 25 | 38 to 40 | 11 to 12 |
| 6 a. m. to 6 p. m., 12 hours | 14 to 15 | 14 to 15 | 17 to 18 | 23 to 24 | 8 to 10 |
| Full daylight, 12½ to 15 hours | 18 to 20 | 40 to 44 | 42 to 44 | 54 to 58 | 14 to 15 |

[a] The relatively greater heights in proportion to the number of hours in the total daily exposures under this treatment are due to the fact that in this case the length of the growing period was not materially shortened by forced earliness in blossoming; they are not to be ascribed to an increased rate of growth.

It may be worthy of note that in the tests under controlled conditions the height of the Biloxi plants under a 12-hour light exposure was practically the same as that of the latest field plantings shown in figure 3, while that of the controls was about the same as that of the early field plantings.

Since in many cases the length of the growing period was greatly curtailed by the forcing action of reduced light exposure on reproduction, the amount of growth was necessarily limited thereby in those plants having a determinate type of inflorescence; but, in addition, measurements made when the blossoming stage of the forced plants had been reached show that the rate of growth was greater as the length of the exposure to light increased. The measurements of height recorded under the several tests relate to the final heights attained by the plants. In the species tested no exceptions to the foregoing principle were encountered; but it is possible, of course, that other species will be found to act differently. It has been demonstrated by a number of investigators that when many green plants are transferred from light to darkness the immediate effect is an acceleration in the rate of growth; and, conversely, the first effect of exposure to light is a retarding of growth. These facts, however, bear on necessary relation to the total effect on rate of growth over a considerable period of time produced by differences in the relative length of night and day.

It remains to be pointed out that striking differences in sensitiveness to decreased length of the daily exposure to light were observed in the different species under investigation. Aside from considerable reductions in the rate of growth and slight chlorosis, soybeans, tobacco, aster, and some others showed no ill effects from the reduced length of illumination, while Hibiscus was not able to make any appreciable growth with the illumination period reduced to nine hours, and lettuce was much more seriously affected, all individuals having perished without making any material growth.

## LENGTH OF DAILY LIGHT EXPOSURE IN RELATION TO SEXUAL REPRODUCTION

While the rate of growth of the species tested was markedly affected by change in the length of the daily illumination period, the effects on blossoming and fruiting are particularly interesting and important. The experiments with soybeans included four varieties which range from early to very late in maturing under normal conditions when grown in the latitude of Washington, D. C. Thus, for plantings in the field extending through the month of May the average number of days from germination to blossoming was approximately 27, 56, 70, and 105, respectively, for the Mandarin, Peking, Tokyo, and Biloxi, the last-named showing no open blossoms till early September. Table III brings out several important facts regarding the effects of reduced light exposure on these four varieties.

TABLE III.—*Number of days required by soybeans to reach the flowering stage under daily light exposures of different lengths*

| Length of daily exposure. | Mandarin. | | | Peking. | | |
|---|---|---|---|---|---|---|
| | Date of germination. | Date of transfer to dark house. | Time from germination to blossoming. | Date of germination. | Date of transfer to dark house. | Time from germination to blossoming. |
| | | | *Days.* | | | *Days.* |
| 10 a. m. to 3 p. m., 5 hours | May 17 | May 20 | [a] 23 | May 17 | May 20 | [a] 23 |
| 9 a. m. to 4 p. m., 7 hours | do | do | 21 | do | do | 21 |
| Do | | | | do | June 7 | 22 |
| Daylight to 10 a. m. and 2 p. m. till dark, 8½ to 11 hours. | | | | June 19 | 19 | 40 |
| 6 a. m. to 6 p. m., 12 hours | June 16 | June 11 | 21 | 16 | 11 | 21 |
| Full daylight, 12½ to 15 hours | May 17 | Control | 26 | May 17 | Control | 62 |
| Do | June 16 | do | 28 | June 16 | do | 51 |

| Length of daily exposure. | Tokyo. | | | Biloxi. | | |
|---|---|---|---|---|---|---|
| | Date of germination. | Date of transfer to dark house. | Time from germination to blossoming. | Date of germination. | Date of transfer to dark house. | Time from germination to blossoming. |
| | | | *Days.* | | | *Days.* |
| 10 a. m. to 3 p. m., 5 hours | May 17 | May 20 | [a] 24 | May 17 | May 20 | [a] 27 |
| 9 a. m. to 4 p. m., 7 hours | do | do | 24 | do | do | 26 |
| Do | do | June 7 | 27 | June 15 | June 24 | 28 |
| Daylight to 10 a. m. and 2 p. m. till dark, 8½ to 11 hours. | June 19 | 16 | 62 | 29 | 16 | 79 |
| 6 a. m. to 6 p. m., 12 hours | 16 | 11 | 28 | 16 | 11 | 28 |
| Full daylight, 12½ to 15 hours | May 17 | Control | 73 | May 17 | Control | 120 |
| Do | June 16 | do | 66 | June 16 | do | [a] 90 |

[a] In those cases in which the plants were placed in the dark house after they had germinated, only the period elapsing after they had been transferred is taken into account, rather than that beginning with the date of germination.

It is seen that when the daily illumination consists of a single exposure of 12 hours or less, the usual length of the growing period from germination to blossoming is only slightly shortened in the early variety, Mandarin; but the shortening effect is increasingly accentuated as the usual growing period increases, till, in the very late variety, Biloxi, this period is reduced to less than one-fourth that of the control plants grown under full daylight exposure during the summer months. In reality, all varieties become early maturing ones under these conditions, and there is but little difference in the time required by the four varieties to reach the blossoming stage. These tests also show that reducing the length of the illumination period below 12 hours has no further effect in shortening the vegetative period, so that apparently there is a certain minimum period of light exposure, reduction of which is without action in hastening the appearance of the flowering stage. These results seem to indicate further that for each variety a certain minimum period of time (ordinarily one of vegetative activity) must elapse from the inception of the stimulating action resulting from the reduced light exposure before the flowering stage can be attained. The data in Table III suggest

that this minimum formative period is approximately 21 days for the Mandarin and Peking varieties, 24 days for the Tokyo, and 26 days for the Biloxi, although under suitable conditions these periods might possibly be somewhat further shortened.

Subjecting the plants to two periods of illumination daily, whereby the total daily exposure averaged 9 or 10 hours, was vastly less effective in inducing early blossoming than a single daily exposure of 12 hours; and, in fact, in the later varieties the effect was of little significance. This is true in spite of the fact that the plants were in darkness during the hours of most intense sunlight—namely, from 10 a. m. to 2 p. m. Obviously it is not merely the total number of hours of sunshine received daily by the plant that may induce such marked shortening of the vegetative period, but the continuity of the exposure also plays an important part. The two plantings of soybeans serving as controls, which first appeared above ground on May 17 and June 16, respectively, did not respond in the same manner to the prevailing seasonal conditions. The vegetative period of the Mandarin was lengthened by two days as a result of the later planting, while the later maturing varieties were affected in the reverse manner. These results are in accord with the fact that the average length of day during the vegetative period was longer for the later planting than for the earlier in the case of the Mandarin, while the reverse is true of the other varieties. The marked action of a decrease in the length of the day, within certain limits, in hastening the arrival of the blossoming stage is equally in evidence throughout the stages of seed formation and maturation. This fact is shown by numerous tests; but experiments (a) (1) and (b) (3) with the Mandarin and Peking varieties, respectively, may be cited specifically.

These tests under controlled conditions clearly show that so far as concerns sexual reproduction the Mandarin soybean is adapted to a relatively long day, since the time required by it to reach the blossoming stage during the long summer days can not be greatly reduced by shortening the length of the daily exposure to light. On the other hand, the Biloxi is distinctively a "short day" variety; and with a daily light exposure of 12 hours or less it blossoms almost as early as the Mandarin, whereas the control plantings show that it refuses to blossom during the long summer days when normally exposed to the light. It is interesting to note that, on the basis of these results, all of the four varieties tested should behave similarly when grown under a 12-hour day such as prevails at the equator. The action of the shortened period of daily light exposure in promoting sexual reproduction offers a satisfactory explanation of the fact that there is a marked progressive shortening of the vegetative period in successive plantings of medium and late maturing varieties of soybeans made during the summer months. In this connection an examination of figure 1, showing graphically this progressive shortening in the vegetative period, is of interest. It should be pointed

out here that the progressive decrease in the length of the vegeta tive period of all varieties apparent in the very early plantings which germinated during the early part of May is probably due to a gradual reduction in the retarding action of relatively low temperatures which prevailed at the time. Again, there is distinct evidence of the retarding influence of lower temperatures on the very latest plantings of the Peking and Biloxi varieties. Eliminating these portions of the curves from consideration, it is evident that the graph for the early variety, Mandarin, is practically horizontal, while there is a marked downward trend in the graphs for the remaining varieties which increases in pitch as we pass toward the later varieties, the drop being quite precipitate in the curve of the very late variety, Biloxi. There is, in short, a marked tendency for the graphs to converge toward a common point as the summer season advances, a fact which is in full accord with the results of the tests under controlled conditions. Another interesting feature of these curves is that for the period around May 25 to June 15 there is a more or less well defined "hump" which is most strongly developed in the curve for the Peking, less prominent in that for the Tokyo, and hardly apparent in the curves for the Biloxi and the Mandarin. A possible explanation of this relative lengthening of the vegetative period of the Peking and Tokyo plantings which germinated during the close of May and early June is to be found in the fact that these plants received the longest possible average light exposure. This would not affect the Mandarin or the Biloxi, since the length of the day is well above the "critical" for the Biloxi and below it for the Mandarin. Apparently field plantings can not be extended through the season in such a way as to bring the plants throughout the vegetative period under a light exposure below the critical in length and at the same time secure throughout the period a sufficiently high temperature (and possibly other favorable factors) to reduce the length of the vegetative period to that which experiments conducted under controlled conditions have established as apparently the physiological minimum requisite for sexual reproduction. There can be no doubt that decreasing temperature, within limits, will retard vital activities of the plant; and the fact should be emphasized that, as a rule, the action of decreasing temperatures as fall approaches must be retarding rather than accelerating in its influence on the attainment of the flowering stage by the plant. It should be pointed out here that the hastening effect of the shorter days on the final maturation of the seed of the soybeans is shown by the fact that in the late plantings there is an evident tendency for the early Mandarin and the later Peking varieties to progress toward maturity at the same rate.

As regards the critical length of day required for furnishing the stimulus which brings into expression the processes of sexual reproduction mentioned above, it should be stated that this has not been determined as yet for any of the plants under study, and it is not possible to state how

narrowly defined this maximum length of day capable of inducing sexual reproduction may be. The outstanding fact is that it is quite different for the four varieties of soybeans. In all cases, however, it is in excess of 12 hours.

Coming to tobacco, the contrast in behavior of the Connecticut Broadleaf and the Maryland Mammoth varieties is very striking. Sexual reproduction in the Connecticut Broadleaf is not materially affected by changes in length of day within the seasonal range for the latitude of Washington or southward. On the other hand, the Maryland Mammoth, which is presumably a mutation from a very old variety of Maryland tobacco and appears to be a typical example of gigantism, can not be forced into blossoming during the summer months by any method now known except artificial shortening of the duration of the daily exposure to light, while the character of gigantism is completely suppressed when the plant is grown during the short days of winter. A glance at Table IV shows that shortening the daily light exposure has not materially affected the Connecticut Broadleaf but has been effective in shortening the vegetative period of the Maryland Mammoth. The Cuban type of Mammoth was affected like the Maryland type, but it appears that the former has a somewhat longer vegetative period than the latter under similar conditions. The Maryland type blossoms readily under the influence of a 12-hour light exposure; but there is a suggestion that a time factor is operative here, for the plants seem not to blossom so promptly as when under the 7-hour exposure. It seems probable also that the Cuban Mammoth will blossom under a 12-hour exposure to light. The observation has been made by Lodewijks (17) that a giant type of Sumatra tobacco—grown under the influence of the 12-hour equatorial day—which may reach the extreme height of 24 feet, either does not blossom at all or forms only a few flowers and seeds. Gigantism in tobacco disappears when the plant is brought under the influence of short days such as prevail in the temperate zone during the winter months. *Nicotiana rustica*, so far as tested, behaves like the Connecticut Broadleaf.

*Aster linariifolius*, again, has given clean-cut results under the different light exposures, as is shown in the summarized data of Table IV. Its behavior is strictly comparable with that of the Biloxi soybean and the giant type of tobacco. It is a typical "short-day" flowering perennial. As with the Biloxi soybean, however, this maximum length of day capable of bringing into expression the flowering and seed-formation processes is in excess of 12 hours. Exposure to light twice daily was without effect, for the vegetative period of the test plants, counting from the beginning of the experiment, was 92 days and that of the controls (not shown in Table IV) was 94 days. Here, again, attention is called to the fact that the total daily exposure to light averaged only about 10 hours, and the plants were in darkness during the period of most intense illumination, 10 a. m. to 2 p. m.

TABLE IV.—*Length of the vegetative period of tobacco and aster as affected by the length of the daily exposure to light*

| Length of exposure. | Connecticut Broadleaf. | | Maryland Mammoth. | | Stewart 70-Leaf Cuban. | | *Aster linariifolius.* | |
|---|---|---|---|---|---|---|---|---|
| | Date of transfer to dark house. | Length of vegetative period. | Date of transfer to dark house. | Length of vegetative period. | Date of transfer to dark house. | Length of vegetative period. | Date of transfer to dark house. | Length of vegetative period. |
| | | *Days.* | | *Days.* | | *Days.* | | *Days.* |
| 10 a. m. to 3 p. m., 5 hours. | ..... | ..... | May 14 | 55 to 61 | ..... | ..... | ..... | ..... |
| 9 a. m. to 4 p. m., 7 hours. | June 5 | 43 to 49 | ...do.... | 61 to 78 | ..... | ..... | May 13 | 36 |
| Full daylight, 12 to 15 hours. | Controls | 42 to 47 | Controls | 152 to 160 | ..... | ..... | Controls | 122 |
| 9 a. m. to 4 p. m., 7 hours. | ..... | ..... | May 14 | 52 to 72 | ..... | ..... | ..... | ..... |
| Full daylight, 12 to 15 hours. | ..... | ..... | Controls[a] | 240 to 264 | ..... | ..... | ..... | ..... |
| 9 a. m. to 4 p. m., 7 hours. | May 28 | 46 to 53 | June 10 | 52 to 59 | June 10 | 67 to 84 | ..... | ..... |
| Full daylight, 12 to 15 hours. | Controls | 36 to 44 | Controls | 84 to 101 | Controls | 81 to 90 | ..... | ..... |
| Daylight to 10 a. m. and 2 p. m. till dark, 11 to 8½ hours. | ..... | ..... | ..... | ..... | ..... | ..... | June 16 | 92 |
| 6 a. m. to 6 p. m., 12 hours. | ..... | ..... | June 11 | 76 to 85 | ..... | ..... | 12 | 37 |
| Full daylight, 12 to 15 hours. | ..... | ..... | Controls | 84 to 101 | ..... | ..... | Controls | 101 |

[a] These controls and the test plants having a vegetative period of 52 to 72 days were in 8-inch pots.

The composite *Mikania scandens* L. is of interest as presenting a new type of plants so far as concerns behavior under long-day and short-day conditions. Under short-day conditions which were maintained for nearly 12 months this plant lost its power of blossoming. In other words, the plant became sterile. The early varieties of soybeans and the Connecticut Broadleaf tobacco blossom and fruit freely through the range of seasonal changes in the length of the day which obtains for the latitude of Washington, while the late varieties of soybeans, the giant types of tobacco, and the aster are essentially sterile when under the influence of the long summer days; and Mikania, on the other hand, is sterile during all seasons of the year except summer when long days prevail. It is worth noting that the Mikania was unable to develop flowers during the summer months when kept under the influence of a short daily exposure to light, notwithstanding that it had been growing in the greenhouse for several months previously.

The bean from the Tropics, *Phaseolus vulgaris*, included in the tests, brings us a step nearer to complete sterility in the latitude of Washington (approximately 39°), for whether it is able to blossom here will depend on the early or late occurrence of killing frost. Evidently it could not blossom very far northward of Washington. Under the influence of a 7-hour daily illumination this bean blossomed in 28 days, and one month later some of its seed pods were mature; yet under outdoor conditions

blossoming did not occur till October 11, 109 days after germination. The fact that this plant does not blossom here till the middle of October indicates that the critical length of day for flowering can not be much in excess of 12 hours; and the physiological minimum for the vegetative period appears to be approximately 28 days, about the same as for the Biloxi soybean. This bean would seem to be admirably adapted to tropical conditions.

The writers are informed by Dr. Shoemaker that in tests made by him at Washington this species in the greenhouse blossomed freely during the winter and developed seed. In the spring some of the plants, having been transferred to pots after the tops had been largely removed, were placed out of doors. New shoots developed, and these grew throughout the summer without blossoming. It is clear that this plant behaves like the Mammoth or giant type of tobacco toward differences in the length of day.

Ragweed is still another example of a short-day plant, for, under a 7-hour exposure, the anthers of the staminate heads were shedding pollen freely within 27 days after the beginning of the test, while under outdoor conditions blossoming did not occur till 7 weeks later. Radish is a good example of the type requiring a long day for attainment of the flowering stage, for, like Mikania, it has not been able to blossom under a 7-hour exposure although the test was continued throughout the summer, while under outdoor conditions blossoms appeared one month after germination. Throughout the test the rosette type of leaf development was maintained under the shortened light exposure, and both leaf and root continued to grow; so here, once more, is apparently a manifestation of gigantism. Under the conditions of the tests, the two biennials, cabbage and carrot, showed no decided response to shortened light exposure so far as concerns flowering; but their behavior under normal conditions indicates that they are to be regarded as typically long-day plants. Hibiscus is a striking example of a long-day plant, for not only is it unable to blossom under a 7-hour light exposure but it is also unable to make any appreciable growth under these conditions. The behavior of Viola is of interest because of the habit of forming both cleistogamous and chasmogamous flowers, the two types appearing at different seasons. It appears that the later developing cleistogamous flowers are to be regarded as forming the more distinctively reproductive organs. Under a 7-hour light exposure, which was not begun till June 7, the plants showed open, purple, petalliferous flowers during the first week in July, although, of course, a previous crop of these blossoms had been produced earlier in the season. The cleistogamous blossoms appeared also on the plants at the usual time, in June. The early goldenrod used in the tests showed no shortening of the vegetative period under a 7-hour exposure.

RELATIONSHIPS BETWEEN ANNUALS, BIENNIALS, AND PERENNIALS

It is well known that there are no hard and fast lines of distinction separating annuals, biennials, and perennials; for plants may change from one of these types to another under influences of environment, although in the past the particular factors of the environment involved have not for the most part been understood. The experiments recorded in this paper make it clear that in any particular region the relative lengths of the days and nights running through the year constitute one of the controlling factors in determining the behavior of plants in this particular. The soybean is commonly regarded as a typical annual in that its entire life cycle is completed in a single season, and coincident with or soon following the maturation of the seed the plant as a whole perishes. As recorded on page 567, however, a suitable change in the length of the daily exposure to light revived the vegetative life of the matured plants. After the first crop of seed had ripened and the foliage had yellowed just as usual immediately before the plant died, new shoots developed on the old stems, vegetative activity was resumed, and, finally, with the approach of the shorter days of autumn, the plants blossomed and fruited a second time. Thus, under controlled conditions the plant simulated the behavior of a flowering perennial except that the two cycles of alternate vegetative and reproductive activity have been crowded into a single season. Ragweed behaved in essentially the same manner. To make the analogy more convincing, attention is directed to the fact that aster, a flowering perennial, under the same treatment gave exactly the same results as the soybeans and ragweed. Thus, the aster readily completed two complete annual cycles within a period of about four months, except that, in the absence of low temperature, the original growth above ground, of course, was not killed. Moreover, in the second period of vegetative activity new shoots were sent up from the roots in addition to the new axillary shoots appearing on the original stems. The first flowering and fruiting of the soybeans, ragweed, and aster were forced by artificially shortening the length of the day. When the plants were restored to the full exposure of the normal summer day, vegetative activity was resumed, and, finally, the natural shortening of the days in August and September resulted in the second flowering and fruiting periods. The factor of the environment which makes the cycle of alternating vegetative and reproductive activities an annual event would thus seem to be the annual periodicity in the length of day. If temperature differences are assumed to be the primary factor, annual periodicity in tropical regions (not including the immediate vicinity of the equator) is not readily explainable.

As has already been pointed out, the Mammoth or giant type of tobacco behaves as a typical flowering annual, like the ordinary tobaccos, when grown under the influence of days not exceeding 12 hours in length. During the winter months the plant blossoms readily and, in fact, becomes practically an ever-blooming type. It is an interesting fact, however,

that as the seed capsules mature the seed-bearing stem dies back only to the first node which may have sent up a new branch. This holds true even though the new branch be but a few inches below the seed head. The portion of the stem below the new branch and the root system henceforth function as parts of a new plant. In winter the new branch blossoms and fruits promptly, perishes, and is succeeded by new branches. As spring advances the new branches coming out assume the giant or nonflowering type of growth which continues till fall brings a return of the short days, when blossoms promptly appear. It would seem that the new branch acts as a rejuvenating or a protective agent against the death of the older organs to which it is attached. Obviously the Mammoth tobacco resembles both the annual and the perennial types of plant life. The sharpness with which the new branch controls the extent of the dying-back of the mother stem is shown in Plate 76, A.

In the latitude of Washington the radish is an annual unless planted very late in the season. It has already been shown that under a shortened light exposure, on the other hand, while vegetative development may continue, flowering does not occur. It would appear from this that the radish might not flower in regions where the maximum length of days is relatively short; and, in fact, according to Dr. Walter Van Fleet, of the Bureau of Plant Industry, the radish as a rule does not blossom when grown in the equatorial region. Similarly, the radish blossoms only occasionally as far north as Porto Rico, where the principal growing season is during the winter months (*13*). This behavior of the radish, again, is obviously an approach toward the nonflowering type of perennial. Similarly, Dr. Van Fleet states that a lima bean coming under his observation in the Tropics had continued to grow as a perennial for a number of years, having attained giant proportions, while there was only occasional and sparse fruiting. Conversely, the beet ordinarily is a biennial in the latitude of Washington, but when grown in Alaska where the summer days are very long, it is likely to develop seed and thus complete its life cycle in a single season. The intimate relationship existing between the length of day and the attainment of the reproductive stage is strikingly shown by the behavior of the radish under special conditions. In the box of plants used as controls in the experiment described on page 565 and discussed above, the great majority of the individuals developed normal flowering stalks and seed pods in due season (see Pl. 75, B). A few individuals, however, developed considerably later, because of delayed germination or some other reason; and these delayed plants began the formation of flowering stalks. The length of the day having decreased to the critical length, the growth of the seed stalk was arrested after a height of a few inches was attained; and instead of the normal flower head, a crown of foliage leaves developed, as shown in Plate 69, B, thus indicating the resumption of vegetative activity. What is believed to be another example of the directing

action of relative day length is the behavior of certain northern varieties of pepper (Capsicum) when planted in Porto Rico in the spring months (*13*). Under these conditions the peppers imported from the higher latitudes of the United States were able to form only a very few fruits before they began to yellow and shed their foliage, after which the plants soon perished. Also, it is stated that the radish when grown in Porto Rico during the winter months behaves as it does when grown nearer the equator. The above-mentioned experimental results and observations seem to justify the conclusion that the relative length of the day through the year is a factor of the first importance in determining whether many plants behave as annuals, biennials, or perennials, and whether reproduction in such plants is vegetative or sexual or both in any particular region.

The forcing of two flowering periods in a single season under controlled conditions naturally directs attention to another phase of periodicity in plant activity—namely, the appearance of the blossoming period in both spring and fall, or only in one of these seasons in regions outside the Tropics. This question is of special interest with respect to perennials. It is apparent that plants blooming only in the spring or fall or in both seasons are to be regarded as requiring relatively short days for attaining this stage. In annuals, ordinarily a period of vegetative development must necessarily precede flowering, so that the latter stage is likely to be deferred till autumn; but when propagation is by means of bulbs or other reproductive storage organs, blossoming may well occur in the spring. In hardy shrubs and trees a typical condition is that in which the formation of flowers or flower buds is inaugurated in the autumn under the influence of the shortening days, while the flowering process is interrupted before completion through the intervention of cold weather. The result is that actual blossoming usually takes place in the spring; but if the fall or early winter temperatures are abnormally high, the flowering process may be completed before cold weather intervenes. This phenomenon is occasionally observed in the apple. In the spring, temperature would be the chief factor in determining the date of blossoming for this class of plants. It is suggested that the seasonal distribution of flower-bud formation in the lemon which is considered in a recent interesting article by Reed (*22*) may be due to these light and temperature relations. The process is most active during the late fall and again in very early spring, with a winter period of low activity. Throughout the summer period of long days, also, activity is at a minimum.

## LENGTH OF DAY CONTRASTED WITH LIGHT INTENSITY

As early as 1735 Reaumer (*21*) undertook to make accurate comparisons of the total quantities of heat required to bring plants to given stages of maturity. At intervals since that time this idea has been

revived, and serious efforts have been made to establish some form of quantitative relationship between plant development and the quantity of heat received from the sun. The work of Linsser (*15*, *16*) and of Hoffman (*11*, *12*) in this field is worthy of special mention. In this connection, also, Abbe's critical review of investigations having to do with the relations between climates and crops is of interest (*1*). It is believed that the results of the present investigation have an important bearing on the subject. Since the quantity of solar radiation received directly by the plant is the product of the intensity and the length of the exposure, it might be expected that any relationship existing between plant processes and the total quantity of radiation received would be disturbed by changes in either the intensity of the light or the duration of the exposure to its action. It has been shown that the relative length of the day is a factor of the greatest importance in relation to reproductive processes in the plant, and it will be of interest to consider whether the intensity of the solar radiation is also of special significance. At the outset it may be observed that it hardly seems likely that light intensity could exert a controlling influence on reproduction in plants, in view of the extent to which the response of plants to differences in light intensity has been studied by investigators without discovery of any very significant relationships so far as concerns reproduction. In the experiments discussed in preceding paragraphs it was found that where daily exposures of 7 hours and 12 hours, respectively, were equally effective in shortening the vegetative period, a total daily illumination aggregating on an average 9 to 10 hours but consisting of two separate exposures, with a 4-hour period of darkness intervening, was vastly less effective in this respect. This shows at once that the total quantity of radiation received can not be responsible for the shortening of the vegetative period produced by shortening the single daily exposure to light. Furthermore, since in the double daily exposures the intervening period of darkness to which the plants were subjected, 10 a. m. to 2 p. m., was at the time of day when the intensity of the solar radiation reaching the earth's surface is at its maximum, the average intensity of the radiation received by these plants is less than that received by those plants which were exposed continuously from 9 a. m. to 4 p. m.

The Stewart Cuban Mammoth tobacco which requires a day length of 12 hours or less to attain the blossoming stage has been grown commercially to some extent under an artificial shade of coarse cheesecloth estimated to reduce the intensity of the sunlight by approximately one-third. It has been observed that this shade has had no noticable effect on the date of blossoming of the tobacco. Again, the aster used in the present investigation grows in the wild state under a variety of situations, some of which are very shaded, but observation during the past

season showed that there was no appreciable difference in dates of flowering under these varied exposures.

Further evidence on this subject is furnished by the following experiments in which soybeans were subjected to different degrees of shading, primarily for determining the effect on oil formation in the seed. Different types of shade were employed, and in some instances shading was combined with regulated differences in the water supply of the soil. In all these experiments the aim has been to use a type of shade which would reduce to a minimum secondary effects, such as modifying the air temperature and the temperature and moisture content of the soil. The object, in short, was to measure, as far as practicable, only the direct action of different light intensities on the plant itself, though, of course, this goal can not be fully attained. With this aim in mind the triangular type of shade, shown in Plate 76, B, was used in a series of tests made in 1916. For this shade the standard cheesecloth of best grade, extensively used for surgical dressings, was employed (see Pl. 77, E). The opening extending around the shade near the top, with loose overhanging flap, is for the purpose of facilitating ventilation. The arrangement is such that the frame of the shade can be raised from time to time to accommodate the growth of the plants. The width of the frame was 4 inches at the base and 18 inches at the top, and it was 30 inches high. In these as in the later tests the Peking variety of soybean was used. It will be recalled that this variety is quite sensitive to changes in the length of the day.

The simplest and perhaps the most satisfactory type of shade was that employed in 1917 and 1918. A frame of iron pipe, 30 inches high, 40 inches wide, and of the desired length, was used to support the cloth. The shades in all cases extended almost due east and west. The beans in each instance were planted in a row 6 inches to the north of the center line of the shade to allow for the southerly swing of the sun's course through the sky. Comparatively open, loosely woven cloth, of the type used for the commercial culture of cigar-wrapper tobacco in New England and Florida, was used for this shade. Four different weaves of cloth were used—6 by 6, 8 by 10, 12 by 12, and 12 by 20 mesh, these figures indicating the average number of threads to the linear inch. These cloths are shown in natural size in Plate 77, A–D.

In 1918 tests were extended to include differences in water supply in combination with three different degrees of shading (see Pl. 78, A). This was accomplished by planting the beans in wooden boxes 24 feet long, 12 inches wide, and 14 inches deep, each box being divided by partitions into three 8-foot sections. These boxes were set in the soil so as to extend about 2 inches above the surface and were filled with soil up to 2 inches of the top. Under each degree of shading, three different soil-moisture contents were maintained, designated as wet,

medium, and dry. Rainfall was largely excluded by laying boards over the boxes on each side of the plants, the boards having sufficient pitch outward to turn the flow of the water. In addition, control plantings were made in the field, a portion without shade and the remainder covered with the shade cloths; and these received no water except the rainfall. Only those features of the test which relate to shading will be considered here, details of the differences in water supply and their effects pertaining more properly to the next section of the paper. To ascertain whether the simplified form of shade exerted any decided indirect effect through the soil, soil thermographs were installed in the soil at a depth of 3 inches under the 12 by 20 cloth shade, in a position near the plants and in a similar position on the field row receiving no special treatment. No significant differences in the temperature records were obtained.

A matter of special importance, of course, is the degree of shading produced by the different types of shade and different weaves of cloth used. For several reasons only approximations can be had as to the intensity of the light received by the plants under the shades. The positions of different plants and different parts of the same plant with respect to the light necessarily vary, and the shape of the shade involves a constantly changing transmission rate by the shade cloth. The normal daily range in light intensity is magnified by the shade, since the coefficient of transmission of the cloth is greatest at midday and decreases toward sunrise and sunset. In the 1916 type of shade there is a relatively small coefficient of light transmission furnished by the sloping side walls covered with cheesecloth. In the simplified type of shade only the transmission through the top comes into consideration, since there are no side walls. The southward extension of the top is such, however, that only diffuse light reaches the plants from the side, with the exception of their extreme lower portions, which are exposed to the direct sunlight in the early morning and late afternoon. In the open type of shade, diffuse light naturally becomes a larger factor. Observations made by Prof. H. H. Kimball, of the United States Weather Bureau, by means of the pyrheliometer gave transmission coefficients of 0.441, 0.292, 0.452, 0.613, and 0.727, respectively, for cheesecloth 12 by 20, 12 by 12, and 8 by 10, and for 6 by 6 mesh netting when exposed normally to the sun's rays. Formulas also were developed by Prof. Kimball which make it possible to compute the shading effect at any hour of the day and for any date. Since the sun's rays never strike the shade cloth at normal incidence, the maximum intensity of the transmitted light, which is attained at midday, is slightly less than indicated by the above values. The computed shading effect produced by each type of netting at various hours of the day on June 1, July 1, and August 1 is shown in Table V. It is seen that for horizontal exposures the shading effect is almost constant from 10 a. m. to 2 p. m. but increases considerably from 10

a. m. to 8 a. m. and from 2 p. m. to 4 p. m. and increases very rapidly from 8 a. m. to 6 a. m. and from 4 p. m. to 6 p. m. For vertical exposures the reverse relations, of course, obtain.

TABLE V.—*Computed shading effect of netting of various weaves and of cheesecloth at different hours of the day during the summer months, with horizontal exposure of the netting and cheesecloth and also with vertical exposure of the cheesecloth*

[Complete shading represented by unity]

| Kind of material. | June 1. | | | | July 1. | | | | August 1. | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Noon. | 10 a. m. and 2 p. m. | 8 a. m. and 4 p. m. | 6 a. m. and 6 p. m. | Noon. | 10 a. m. and 2 p. m. | 8 a. m. and 4 p. m. | 6 a. m. and 5 p. m. | Noon. | 10 a. m. and 2 p. m. | 8 a. m. and 4 p. m. | 6 a. m. and 6 p. m. |
| 6 by 6 netting | 0.30 | 0.30 | 0.37 | 0.66 | 0.29 | 0.31 | 0.36 | 0.61 | 0.30 | 0.31 | 0.37 | 0.69 |
| 8 by 10 netting | .47 | .43 | .51 | .90 | .47 | .42 | .50 | .83 | .41 | .43 | .51 | .94 |
| 12 by 12 netting | .56 | .58 | .69 | 1.0 | .55 | .58 | .78 | 1.0 | .56 | .59 | .69 | 1.0 |
| 12 by 20 netting | .69 | .71 | .83 | 1.0 | .68 | .71 | .81 | 1.0 | .69 | .72 | .84 | 1.0 |
| Cheesecloth (top) | .57 | .59 | .70 | 1.0 | .57 | .59 | .69 | 1.0 | .56 | .59 | .71 | 1.0 |
| Cheesecloth (vertical sides) | 1.0 | .78 | .62 | .57 | 1.0 | .81 | .63 | .57 | .96 | .77 | .62 | .57 |

To obtain further information as to the shading effect of the nettings used, a section of the simplified type of shade, without side covering, was set up and covered with the 12 by 12 netting. Under this shade (about 6 inches below the netting) Livingstone standardized black and white spherical atmometer cups were installed, and corresponding control cups were placed in full sunlight in the open air. In general, it was found that satisfactory results could not be secured when the wind was blowing; but when there was no appreciable breeze, readings were obtained which seemed to indicate a coefficient of light transmission reasonably close to that determined by Prof. Kimball. Typical readings obtained on clear, calm days are given in Table VI.

TABLE VI.—*Readings of black and white spherical atmometer cups under 12 by 12 netting and in direct sunlight, and the indicated coefficient of light transmission, 1919*

| Date. | Period of exposure. | Readings. | | | | Difference. | | Indicated coefficient of light transmission for 12 by 12 net. |
|---|---|---|---|---|---|---|---|---|
| | | Under the net. | | In the open. | | Under the net. | In the open. | |
| | | Black cup. | White cup. | Black cup. | White cup. | | | |
| | | *Cc.* | *Cc.* | *Cc.* | *Cc.* | *Cc.* | *Cc.* | |
| Aug. 26 | 10.45 a. m. to 11.45 a. m. | 4.8 | 3.5 | 6.0 | 3.7 | 1.3 | 2.3 | 0.56 |
| 26 | 10.45 a. m. to 3 p. m. | 24.3 | 18.0 | 29.6 | 19.5 | 6.3 | 10.1 | .62 |
| 28 | 9 a. m. to 3 p. m. | 20.7 | 14.4 | 26.9 | 15.8 | 6.3 | 11.1 | .56 |
| 29 | 10.15 a. m. to 3 p. m. | 18.2 | 12.8 | 22.4 | 13.0 | 5.4 | 9.4 | .57 |

In the 1916 experiments the soybeans were planted June 21, and the shade was placed in position July 5. Detailed observations were made on the growth and development of the shaded plants and of the unshaded controls. There were 93 individuals under the shade and 67 in the

control row. The summarized data in Table VII will bring out the comparative behavior of the shaded and unshaded plants.

TABLE VII.—*Effect of shading soybeans with cheesecloth, 1916*

| Treatment. | Average height. | Air-dry weight per stalk, defoliated. | Yield of beans per stalk. | Yield of hulls per stalk. | Percentage of beans in seed pods. | Date of blossoming. |
|---|---|---|---|---|---|---|
| | | *Gr.* | *Gr.* | *Gr.* | | |
| Plants shaded | 3 ft. 5 in. | 5.4 | 10.5 | 5.4 | 66.1 | Aug. 7 |
| Plants not shaded | 2 ft. 3 in. | 9.9 | 17.0 | 9.0 | 65.2 | Do. |

The shaded plants show the typical effects of reduced light intensity so often observed—increased elongation of stem, slender growth, enlarged area of leaves, reduced production of dry matter. Besides these effects the yield of seed was considerably reduced. For present purposes the important fact is that although the maximum intensity of the direct light reaching these plants was only about 43 per cent of the normal, the date of blossoming was not affected in the slightest degree. This is a striking contrast with the fact that by reducing the length of the daily light exposure from an average of approximately 14 hours to 12 hours, or about 15 per cent, the length of the period from germination till blossoming was reduced from 51 to 21 days. It was observed, however, that the seeds of the shaded plants were about a week later than those of the control plants in reaching final maturity.

In the 1917 tests the beans were planted June 27 and the shades placed in position a few days after germination for the first series, while in a second series the shades were set up at the time of blossoming. Two grades of netting were used, the 6 by 6 and the 8 by 10 mesh. The general behavior of the plants is shown in Table VIII. Here, again, it is seen that reducing the intensity of the direct sunlight to maxima of about 70 and 59 per cent, respectively, of the normal has shown no effect on the date of flowering.

TABLE VIII.—*Effect of shading soybeans with 6 by 6 and 8 by 10 mesh cotton netting, 1917*

| Treatment. | Number of individuals grown. | Average height. | Air-dry weight per stalk, defoliated. | Yield of beans per stalk. | Yield of hulls per stalk. | Percentage of beans in seed pods. | Date of blossoming. |
|---|---|---|---|---|---|---|---|
| | | *Inches.* | *Gr.* | *Gr.* | *Gr.* | *Gr.* | |
| 6 by 6 netting from germination to maturity | 72 | 28 | 4.7 | 9.4 | 5.1 | 64.6 | Aug. 17 |
| 6 by 6 netting from blossoming to maturity | 67 | 24 | 5.8 | 9.9 | 5.0 | 66.8 | Do. |
| 8 by 10 netting from germination to maturity | 75 | 25 | 3.7 | 7.0 | 4.1 | 62.9 | Do. |
| 8 by 10 netting from blossoming to maturity | 65 | 25 | 5.4 | 9.4 | 5.4 | 63.4 | Do. |
| Not shaded | 305 | 22 | 4.8 | 8.5 | 5.1 | 62.7 | Do. |

TABLE IX.—*Effect of various degrees of shading in combination with differences in water supply on the growth and development of soybeans, 1918*

| Treatment. | | | Number of plants grown. | Average height. | Weight per stalk, defoliated. | Weight of hulls per plant. | Weight of beans per plant. | Percentage of beans in seed pods. |
|---|---|---|---|---|---|---|---|---|
| Shade. | Moisture. | Duration. | | | | | | |
| | | | | *Inches.* | *Gr.* | *Gr.* | *Gr.* | |
| 12 by 12 netting | Wet | Germination till maturity. | 40 | 31 | 9.8 | 8.4 | 14.5 | 63.5 |
| Do | Medium | do | 42 | 26 | 6.1 | 5.6 | 10.2 | 64.6 |
| Do | Dry | do | 44 | 21 | 3.4 | 3.5 | 6.3 | 65.8 |
| 6 by 6 netting | Wet | do | 45 | 31 | 9.6 | 8.5 | 14.3 | 61.8 |
| Do | Medium | do | 47 | 28 | 6.7 | 6.7 | 11.4 | 63.0 |
| Do | Dry | do | 48 | 21 | 3.1 | 3.1 | 6.9 | 69.4 |
| 12 by 12 netting | Actual rainfall. | do | 63 | 31 | 9.4 | 8.1 | 15.7 | 66.1 |
| 6 by 6 netting | do | do | 58 | 31 | 9.6 | 8.6 | 16.0 | 65.6 |
| 12 by 20 netting | do | do | 47 | 34 | 9.3 | 7.5 | 15.0 | 66.9 |
| Not shaded | do | do | 110 | 26 | 9.9 | 8.5 | 16.4 | 65.7 |
| Not shaded[a] | do | do | 77 | 32 | 13.5 | 10.5 | 24.8 | 70.2 |
| 12 by 12 netting | Wet | Blossoming till maturity. | 43 | 28 | 7.7 | 6.3 | 14.5 | 69.9 |
| Do | Medium | do | 45 | 30 | 7.8 | 7.1 | 13.1 | 65.0 |
| Do | Dry | do | 45 | 29 | 7.0 | 6.8 | 11.0 | 69.5 |
| 6 by 6 netting | Wet | do | 45 | 32 | 8.7 | 6.7 | 13.3 | 66.3 |
| Do | Medium | do | 44 | 31 | 8.3 | 6.5 | 12.7 | 66.3 |
| Do | Dry | do | 44 | 25 | 7.3 | 6.5 | 11.6 | 63.9 |
| Not shaded | Wet | do | 46 | 31 | 7.8 | 7.2 | 13.1 | 64.9 |
| Do | Medium | do | 48 | 32 | 7.9 | 6.3 | 12.3 | 66.2 |
| Do | Dry | do | 48 | 24 | 5.7 | 4.9 | 8.9 | 64.3 |
| 12 by 12 netting | Actual rainfall. | do | 58 | 30 | 10.1 | 8.2 | 16.8 | 67.3 |
| 6 by 6 netting | do | do | 62 | 30 | 10.6 | 9.8 | 17.7 | 64.4 |
| 12 by 20 netting | do | do | 49 | 32 | 9.7 | 8.2 | 16.9 | 67.2 |

[a] This planting differed from the control immediately preceding only in that the plants were spaced 5 to 6 inches apart in the row while in all other cases they were spaced 2 to 3 inches apart.

In the 1918 experiments the plantings were made from June 4 to 6. Two different degrees of shading were used in combination with three different rates of water supply in each of two series, one covering the period from germination to maturation and the other extending only from blossoming till maturation. In addition, two corresponding series were run, in each of which three different degrees of shading were employed without variation in the water supply, the plants in this case being grown in open field rows without use of boxes, so that the actual rainfall of the season was received by the soil. As controls, a series was arranged without shade but with the three rates of water supply, which extended only from the blossoming period till maturation, the plantings being in buried boxes as in the other experiments having to do with water supply. An additional control consisted of a planting in the field without any special treatment as to either shade or water supply; and, incidentally, a similar planting was made which differed only in that the plants were spaced 5 to 6 inches apart instead of the standard distance of 2 to 3 inches used in all other cases. The shades for the two periods of shading were placed in position, and the special water treatments were begun on June 12 and 13 and August 9, respectively. The results of the tests are summarized in Table IX. It appears that the effect of the shade on the size, weight, and relative proportions of the plant parts is

dependent to a considerable extent on the relative water supply. In general, however, reduction in light intensity during the period from germination till maturity gives results similar to those obtained in the preceding tests; and there is a tendency toward a reduced yield of seed, as previously noted. Reducing the intensity of light during the period between blossoming and final maturity, on the other hand, appears to increase somewhat the yield of seed. Without exception, the plants began blossoming on August 7 under all treatments as to shade and differences in water supply, applied either singly or in combination. In these tests it is estimated that under the heaviest shading the maximum intensity of the direct sunlight reaching the plant was only 32 per cent of the normal, and the average for the day could scarcely have exceeded 25 per cent of the normal.

## RELATION OF OTHER FACTORS OF THE ENVIRONMENT TO REPRODUCTION

Having seen that under the conditions of the experiments described in the previous section differences in light intensity were without effect on the length of the vegetative period which preceeds flowering in soybeans, it is worth while considering whether other factors of the environment, especially water supply and temperature, are of significance. In studying the relation of the water supply to the formation of oil in the seed, a number of tests have been made with soybeans, beginning with 1912; but it will suffice to consider here only the results obtained for the years 1916 and 1918 with the Peking variety. In 1916 plantings were made in a series of four boxes set in the soil and provided with board covers, just as has been described in the preceding section (see p. 583). Each of the boxes was 12 feet long, 12 inches wide, and 12 inches deep. In one of these boxes the soil was maintained in a relatively moist condition from germination to final maturity, and in a second one the soil was kept comparatively dry during this period. In the third box the soil moisture was kept the same as that in the first box till the most active flowering stage was past, after which the moisture content was reduced to that of the second box. In the fourth box the soil was kept relatively dry till the flowering stage was past and thereafter in a relatively moist condition. A control planting receiving the actual rainfall was also made in the field. The beans were planted June 21, and the addition of water to the boxes began July 17. The transition in the moisture relations of the third and fourth boxes was begun August 19. The appearance of the plants in the boxes in the late summer is shown in Plate 79, A. The quantities of water supplied to the boxes each week, together with the rainfall for the period of the tests, are given in Table X. Determinations of the moisture content of the soil in the boxes were made at intervals through the month of August. Experience has shown that in the field the soil used in these tests contains 16 to 18 per cent moisture when in best condition

for most crop plants. The results of the moisture determinations in the boxes are shown in Table XI.

TABLE X.—*Quantities of water added to boxes and the rainfall during the period of the tests dealing with effect of differences in soil moisture on the development of soybeans, 1916*

| Week ending— | Box 1, wet from germination to maturity. | Box 2, dry from germination to maturity. | Box 3, wet from germination to blossoming; dry thereafter. | Box 4, dry from germination to maturity; wet thereafter. | Rainfall (on field planting only). |
|---|---|---|---|---|---|
| | *Gallons.* | *Gallons.* | *Gallons.* | *Gallons.* | *Inches.* |
| July 24 | 32 | 0 | 32 | 0 | 1.77 |
| 31 | 20 | 0 | 20 | 0 | 2.14 |
| Aug. 7 | 20 | 0 | 20 | 0 | .56 |
| 14 | 18 | 4 | 18 | 4 | .23 |
| 21 | 18 | 4 | 4 | 12 | .38 |
| 28 | 20 | 2 | 8 | 12 | .92 |
| Sept. 4 | 12 | 4 | 6 | 6 | .03 |
| 11 | 37 | 6 | 6 | 26 | .70 |
| Total | 177 | 20 | 114 | 60 | 6.73 |
| Equivalent to | [a] 23.6 | [a] 2.7 | [a] 15.2 | [a] 8 | ..... |

[a] Inches.

TABLE XI.—*Moisture content of soil in boxes used for growing soybeans, 1916*

| Date of examination. | Box 1, wet from germination to maturity. | Box 2, dry from germination to maturity. | Box 3, wet from germination to blossoming; dry thereafter. | Box 4, dry from germination to maturity; wet thereafter. |
|---|---|---|---|---|
| | *Per cent.* | *Per cent.* | *Per cent.* | *Per cent.* |
| July 17 | 13.0 | 13.0 | 13.0 | 13.0 |
| Aug. 1 | 20.6 | 11.0 | 21.2 | 11.0 |
| 8 | 20.6 | 11.0 | 13.8 | 11.0 |
| 15 | 15.5 | 9.5 | 15.5 | 9.5 |
| 22 | 14.7 | 10.0 | 10.8 | 16.8 |

The comparative growth and development of the plants under the different treatments are indicated by the data presented in Table XII. It appears that the control plants in the field were somewhat larger and considerably more productive than the best plants in the boxes, which were those receiving the larger water supply from germination to maturity. These differences were possibly due to the larger volume of soil available to the plants in the field. There are large reductions in the size and productiveness of the plants in the boxes resulting from a deficiency in the water supply. It appears also that a more favorable water supply during the period preceding the flowering stage resulted in greater vegetative development, while a more favorable water supply after the flowering stage gave a larger yield of seed. In spite of the well-defined

differences in the size of the plants and their fruitfulness brought about by differences in the water supply, the date of blossoming was not affected at all, the first blossoms in all boxes and in the field appearing August 7. No important differences were observed in the time of final maturation under the different treatments.

TABLE XII.—*Effect of differences in the moisture content of the soil on the growth and development of soybeans, 1916*

| Treatment. | Number of plants grown. | Average height. | Air-dry weight per stalk, defoliated. | Weight of seed hulls per stalk. | Weight of beans per stalk. | Percentage of beans in seed pods. |
|---|---|---|---|---|---|---|
| | | *Inches.* | *Gr.* | *Gr.* | *Gr.* | |
| Soil wet from germination to maturity | 64 | 27 | 8.0 | 7.3 | 12.4 | 63.0 |
| Soil dry from germination to maturity | 67 | 19 | 4.1 | 3.1 | 8.1 | 62.4 |
| Soil wet from germination to blossoming and dry thereafter | 69 | 26 | 7.4 | 3.2 | 8.6 | 62.2 |
| Soil dry from germination to blossoming and wet thereafter | 57 | 21 | 5.5 | 6.6 | 11.5 | 63.5 |
| Control, in field under actual rainfall | 67 | 27 | 9.8 | 9.1 | 17.0 | 65.2 |

It may be observed in passing that the wooden boxes placed in the soil as indicated above have been found to be very satisfactory for conducting field tests dealing with the effects of the water supply on plants. By the arrangement of sloping covers on either side of the plants rainfall can be very largely excluded, and losses of soil moisture from causes other than transpiration are reduced to a minimum. Boxes of any convenient size and length may be used, and placing the boxes in the soil insures a close approach to general field conditions.

The general plan as well as a summary of the results of the 1918 tests on the effects of differences in water supply in combination with different degrees of shading have been given in the preceding section on light intensity. It is appropriate to give here further details of the water treatments. The surface area of the soil in each 8-foot section of the boxes was 8 square feet, so that nearly 5 gallons of water would be required to supply the equivalent of a rainfall of 1 inch. The water was applied in measured quantities by means of a garden hose. Although nearly all water lost by the soil was through transpiration, it was found necessary to water heavily each day in periods of hot and dry weather. The quantities of water added weekly and the rainfall during the period of the tests are shown in Table XIII.

Soil moisture determinations were made at intervals during the season from samples taken from the field and from the boxes. The samples were taken to a depth of 12 inches—that is, to the bottom of the soil in the boxes. Composite samples were made up from boxes receiving the same quantities of water. The samples were taken in all cases just before

adding water to the soil, so that the average moisture contents would be somewhat higher than these figures. Results of the moisture determinations are shown in Table XIV.

TABLE XIII.—*Quantities of water added weekly to soybeans, and the rainfall during the period of the tests dealing with effect of differences in soil moisture, 1918*

| Week ending— | From germination to maturity. | | | | | | From blossoming to maturity. | | | | | | | | | Rainfall on controls. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 12 by 12 net shade. | | | 6 by 6 net shade. | | | 12 by 12 net shade. | | | 6 by 6 net shade. | | | Not shaded. | | | |
| | Wet. | Medium. | Dry. | Wet. | Medium. | Dry. | Wet. | Medium. | Dry. | Wet. | Medium. | Dry. | Wet. | Medium. | Dry. | |
| | *Gall.* | *Gall.* | *Gall.* | *Gall.* | *Gall.* | *Gall.* | *Gall.* | *Gall.* | *Gall.* | *Gall.* | *Gall.* | *Gall.* | *Gall.* | *Gall.* | *Gall.* | *In.* |
| June 21 | 0.5 | 0.5 | (a) | 0.5 | 0.5 | (a) | 4.0 | 4.0 | 4.0 | 4.0 | 4.0 | 4.0 | 4.0 | 4.0 | 4.0 | 0.11 |
| 28 | 4.0 | 1.0 | (a) | 4.0 | 1.0 | (a) | 2.0 | 2.0 | 2.0 | 2.0 | 2.0 | 2.0 | 2.0 | 2.0 | 2.0 | .87 |
| July 5 | 9.0 | 7.0 | (a) | 9.0 | 7.0 | (a) | 9.0 | 9.0 | 9.0 | 9.0 | 9.0 | 9.0 | 9.0 | 9.0 | 9.0 | .38 |
| 12 | 3.0 | 2.0 | 1.5 | 3.0 | 2.0 | 1.5 | 4.0 | 4.0 | 4.0 | 4.0 | 4.0 | 4.0 | 4.0 | 4.0 | 4.0 | .17 |
| 19 | 3.0 | 2.0 | 1.0 | 3.0 | 2.0 | 1.0 | 3.0 | 3.0 | 3.0 | 3.0 | 3.0 | 3.0 | 3.0 | 3.0 | 3.0 | 1.41 |
| 26 | 6.0 | 6.0 | 6.5 | 6.0 | 6.0 | 6.5 | 5.0 | 5.0 | 5.0 | 5.0 | 5.0 | 5.0 | 5.0 | 5.0 | 5.0 | .71 |
| Aug. 2 | 8.0 | 8.0 | 3.0 | 8.0 | 8.0 | 3.0 | 7.0 | 7.0 | 7.0 | 7.0 | 7.0 | 7.0 | 7.0 | 7.0 | 7.0 | .69 |
| 9 | 24.0 | 18.0 | 9.0 | 24.0 | 18.0 | 9.0 | 22.0 | 20.0 | 18.0 | 22.0 | 20.0 | 18.0 | 22.0 | 20.0 | 18.0 | .16 |
| 16 | 24.0 | 22.0 | 5.0 | 24.0 | 22.0 | 5.0 | 24.0 | 22.0 | 4.0 | 25.0 | 22.0 | 4.0 | 24.0 | 22.0 | 4.0 | 1.03 |
| 23 | 24.0 | 22.0 | 5.5 | 24.0 | 22.0 | 5.5 | 24.0 | 22.0 | 5.5 | 24.0 | 22.0 | 5.5 | 24.0 | 22.0 | 5.5 | .26 |
| 30 | 30.0 | 20.0 | 8.0 | 30.0 | 20.0 | 8.0 | 30.0 | 20.0 | 8.0 | 30.0 | 20.0 | 8.0 | 30.0 | 20.0 | 8.0 | .44 |
| Sept. 6 | 28.0 | 18.0 | 6.0 | 28.0 | 18.0 | 6.0 | 28.0 | 18.0 | 6.0 | 28.0 | 18.0 | 6.0 | 28.0 | 18.0 | 6.0 | .44 |
| 13 | 8.0 | 6.0 | 2.0 | 8.0 | 6.0 | 2.0 | 8.0 | 6.0 | 2.0 | 8.0 | 6.0 | 2.0 | 8.0 | 6.0 | 2.0 | .51 |
| 20 | 18.5 | 14.0 | 5.5 | 18.5 | 14.0 | 5.5 | 18.5 | 14.0 | 5.5 | 18.5 | 14.0 | 5.5 | 18.5 | 14.0 | 5.5 | 1.77 |
| 27 | 8.0 | 4.0 | 4.0 | 8.0 | 4.0 | 4.0 | 8.0 | 4.0 | 4.0 | 8.0 | 4.0 | 4.0 | 8.0 | 4.0 | 4.0 | .62 |
| Total | 198.0 | 150.5 | 57.0 | 198.0 | 150.5 | 57.0 | 196.5 | 160.0 | 87.0 | 196.5 | 160.0 | 87.0 | 196.5 | 160.0 | 87.0 | 10.47 |
| Equivalent to | (b) 39.6 | (b) 30.1 | (b) 11.4 | (b) 39.6 | (b) 30.1 | (b) 11.4 | (b) 39.3 | (b) 33.3 | (b) 17.4 | (b) 39.3 | (b) 33.3 | (b) 17.4 | (b) 39.3 | (b) 33.3 | (b) 17.4 | ..... |
| For period from Aug. 2 to Sept. 27 | | | | | | | 32.5 | 52.2 | 10.6 | 32.5 | 25.2 | 10.6 | 32.5 | 25.2 | 10.6 | 5.5 |

(a) None. (b) Inches.

TABLE XIV.—*Water content of soil in boxes and in the field during the period of the tests with soybeans, 1918*

| Date of sampling. | From germination to maturity. | | | From blossoming to maturity. | | | | | | In field. |
|---|---|---|---|---|---|---|---|---|---|---|
| | 12 by 12 and 6 by 6 netting. | | | 12 by 12 and 6 by 6 netting. | | | No shade. | | | |
| | Wet. | Medium. | Dry. | Wet. | Medium. | Dry. | Wet. | Medium. | Dry. | |
| | *Per ct.* | *Per ct.* | *Per ct.* | *Per ct.* | *Per ct.* | *Per ct.* | *Per ct.* | *Per ct.* | *Per ct.* | *Per ct.* |
| June 19 | 19.4 | 18.6 | 17.1 | ..... | ..... | ..... | ..... | ..... | ..... | ..... |
| July 1 | 19.5 | 16.4 | 15.3 | 20.6 | 20.6 | 20.6 | 20.6 | 20.6 | 20.6 | ..... |
| 8 | 20.8 | 16.4 | 12.9 | 19.1 | 19.1 | 19.1 | 19.1 | 19.1 | 19.1 | ..... |
| 15 | 21.9 | 18.0 | 14.6 | 18.8 | 18.8 | 18.8 | 20.2 | 20.2 | 20.2 | ..... |
| 23 | 16.7 | 13.1 | 11.3 | 18.1 | 18.1 | 18.1 | 18.3 | 18.3 | 18.3 | ..... |
| Aug. 2 | 17.1 | 12.5 | 10.4 | 16.6 | 16.6 | 16.6 | 15.5 | 15.5 | 15.5 | ..... |
| 13 | ..... | ..... | 10.3 | ..... | ..... | 10.3 | ..... | ..... | ..... | 10.8 |
| 16 | 19.6 | 18.2 | 12.2 | 19.6 | 18.2 | 12.2 | 19.6 | 18.2 | 12.2 | 11.9 |
| 20 | ..... | ..... | 8.4 | ..... | ..... | 10.0 | ..... | ..... | 11.0 | 11.5 |
| Sept. 5 | 22.1 | 18.7 | 11.5 | 22.1 | 18.7 | 11.5 | 22.1 | 18.7 | 11.5 | 8.3 |

The rainfall was relatively light but extraordinarily uniform in distribution during the season; and, though the field soil was comparatively dry most of the time, the plants did not show wilting at any stage. In the boxes the plants in the "dry" sections were kept in a condition in which wilting frequently occurred in the middle of the day through the season. The boxes were 12 inches in width while the distance between field rows was 3.3 feet. It is interesting to note, therefore, that the plants in the boxes, which had slightly less than a third as much lateral soil area from which to draw their moisture as was available to the plants in the field, required an addition of water equal to three times the rainfall in order to attain the same development as was reached by the field plants. When this condition was attained—that is, in the "wet" boxes—the size of the plants was almost exactly the same as that of the plants in the field.

It is seen at once (Table X) that in the boxes the water supply is the chief limiting factor, for the height of the plants, the size of the stalks, the production of seed, etc., are greatly affected by the quantity of the water supplied. On the other hand, reduction of the water supply, even to the point where almost daily wilting of the plants occurred, did not change the time of flowering by a single day. Changing the water supply after the flowering stage likewise produced decided effects on the further development of the plants, and in the same general direction as noted above, although naturally the changes are not so great as when the differences in water supply are maintained throughout the active period of the plant's life. As regards maturation, it was observed that the plants in the wetter soil of the boxes were perhaps a week later in shedding their leaves and ripening their seed pods than those in the field and in the drier soil of the boxes.

While water supply is the chief factor influencing plant development in the boxes, these tests furnish a clear case of the simultaneous action of two limiting factors, for the different degrees of shading likewise affected the development of the plants. Quantitatively, these two limiting factors are of decidedly unequal significance. Within the limits covered by the tests, the effects of the differences in water supply could be demonstrated in nearly all cases even if the light intensity were an uncontrolled variable. On the other hand, the effects of the differences in light intensity would be completely masked in most instances if the water supply were not rigidly controlled. This experiment illustrates the problems of soil productiveness and crop yields which confront the agronomist and clearly points to the futility of attempting to deal with limiting factors of relatively small significance, such as comparatively narrow distinctions in fertilizer requirements of given soils or crops or in the crop-yielding powers of different strains or varieties of plants.

That temperature is a factor of first importance in influencing and controlling plant activities is well understood, and it needs to be considered here only in its relations to the length of day as a factor playing a dominant rôle in the reproductive processes of the plant. It is well known that in accordance with Vant Hoff's law the speed of chemical reactions is doubled for each increase of 5° to 10° in temperature; and similarly plant activities and processes such as respiration and growth are accelerated by increase in temperature, provided the optimum is not exceeded. Conversely, decrease in temperature may moderately retard the plant's activities, or this effect may increase to more or less complete inhibition. Extremes in either direction, of course, may result in killing the flowering buds or fruits, the vegetative shoots, or the entire plant. It is a matter of common knowledge that low temperature retards the development and the unfolding of flowers. An interesting interrelationship of this action of temperature and that of the seasonal decrease in length of day is seen in the behavior of such trees as the apple, previously referred to. Under the influence of the relatively short days fruit trees of this type might be expected to unfold their flowers regularly in the fall instead of in the spring were it not for the interference of low temperatures. The low temperature of winter would seem to have the effect of changing what would otherwise be among the latest flowering plants of the fall into the early flowering ones of spring.

For the temperate and frigid zones the results of the present investigation have made it clear that in some species, at least, distinctions in the time of flowering and fruiting of different varieties, which may be classed as early maturing, late maturing, nonmaturing, and sterile or nonflowering, are due primarily to responses to different day lengths which come into play as the season advances. Here, again, low temperature becomes a factor of increasing importance as the season advances, and, so far as concerns "short-day" plants, it controls the situation with respect to the conditions of nonripening of fruit and of nonflowering. With increasing latitude this relationship between the opposed action of the length of day and the falling temperature becomes more critical for the later maturing varieties. With decreasing latitude a condition is reached in the subtropics which is much more favorable to late maturing or short-day varieties, for the length of day may fall below the critical maximum for flowering without the inhibiting or destructive action of low temperatures coming into play to prevent successful fruiting. At the equator, annual periodicity of both temperature and length of day cease to play an important rôle in plant processes.

## LENGTH OF DAY AS A FACTOR IN THE NATURAL DISTRIBUTION OF PLANTS

In an intelligent understanding of the natural distribution of plants over a particular area those factors which are favorable or unfavorable to growth and successful reproduction for each species must be given

consideration. Heretofore temperature, water, and light intensity relations have been considered the chief external limiting factors governing the distribution or range of plants. In the light of the observations and experimental results presented in this paper it seems probable that an additional factor, the relative length of the days and nights during the growing period, must also be recognized as among those causes underlying the northward or southward distribution of plants.[1] It is evident that the equatorial regions of the earth alone enjoy equal days and nights throughout the entire year. Provided the water relations are favorable, the warm temperatures in these regions favor a continuous growing season for plants. Passing northward from the equatorial regions into higher latitudes, temperatures promoting active vegetative growth and development are restricted to a summer period which, other conditions being equal, becomes progressively shorter as the polar regions are approached. Coincident with these changes from lower to higher latitudes, the summers are characterized by lengthening periods of daylight and the winters by decreasing periods of daylight. We may now consider how these different day and night relations operating during the summer growing period will exercise more or less control upon the northward or southward distribution of certain plants.

It is evident that a plant can not persist in a given region or extend its range in any direction unless it finds conditions not only favorable for vegetative activity but also for some form of successful reproduction. For present purposes only sexual or seed reproduction need be considered. The experiments above described have indicated that for certain plants—for example, ragweed and the aster—the reproductive or flowering phase of development in some way depends upon a stimulus afforded by the shortening of the days and the consequent lengthening of the nights as the summer solstice is passed. It remains to consider more specifically the bearing these facts may have when plants characterized by this type of behavior are subjected to the daylight relations of different latitudes. In the vicinity of Washington, D. C., the ragweeds regularly shed their first pollen about the middle of August. It may be considered that the earliest flowering plants bloom about this date each season because they react to a length of day somewhat less than that of the longest day, which is about 15 hours in this latitude. In other words, as soon as the decreasing length of day falls somewhat below 15 hours, a condition which obtains about July 1, the period of purely vegetative activity is checked, and the flowering phase of development is initiated. Should the seeds of such plants now be carried as far as northern Maine into a latitude of 46° to 47°, these plants would not experience a length of day falling below 15 hours in length, for which it is assumed they are best

[1] In this connection the tables showing the time of sunrise and sunset at 10-day intervals through the year for various latitudes in North America, as given in SMITHSONIAN CONTRIBUTIONS TO KNOWLEDGE, v. 21 (1876), p. 114–119, will be found very convenient for reference.

suited, until about August 1. In this latitude, then, provided other conditions did not intrude, flowering would be delayed until about August 1, and the chances of successfully maturing seed before killing frosts intervened would be greatly lessened. If the seed were carried still farther north, the plants might not blossom at all, owing to the fact that even the shortest days of the summer growing period would exceed those to which they were best suited in their normal habitat. Although in such instances these failures naturally would have been explained in the past on the basis of unfavorable temperature relations alone, it is obvious that length of day, primarily, is the limiting factor which has retarded the reproductive period so that unfavorable temperature relations have intervened to prevent the ripening of seed.

Although the Arctic summers are very short, plants have become successfully established under such conditions, largely by the development of specialized perennial types, which find the extremely long days favorable both to vegetative growth and to flower production. Although it has been usually considered that the purely Arctic forms are confined to Arctic conditions because of certain temperature requirements, etc., it is possible that length of day, hitherto overlooked as a factor in plant distribution, may have much to do with their restricted range apart from other factors of the environment.

In tropical regions it is probable that the success of many native plants is more or less closely dependent upon the conditions of equal or nearly equal days and nights which prevail there during the entire year. The varieties of bean coming from Peru and Bolivia appear to be of this type. It is evident that such plants, whose flowering conditions depend more or less closely upon a length of day little if at all exceeding 12 hours, can not attain the flowering stage attended by successful seed production in higher latitudes, at least during the summer season, which would necessarily be characterized by days in excess of 12 hours. It is indicated by the beans in question, however, that some plants of this class may grow and attain successful seed production under day lengths less than 12 hours. This being the case, such plants could at least extend their range beyond the Tropics in so far as the temperature conditions of the winter months in these latitudes were favorable to growth and reproduction.

In any study of the phenological aspects of different species of plants the fact stands out that certain plants bloom at definite seasons of the year. This is quite as marked in subtropical regions as in more northern regions having a definite summer growing season. In this connection it is probable that the relative lengths of the days and nights are of particular significance in many instances. The behavior of the composite *Mikania scandens*, as observed under specially controlled conditions and under winter conditions in the greenhouse, may be more critically considered in relation to its normal blooming season throughout its range.

This plant normally blooms from late July to middle or late September, indicating that blossoming becomes more or less inhibited as the autumnal equinox is passed in late September and the length of the day falls below 12 hours. In the greenhouse at Washington the short days of the winter, ranging around 9 to 10 hours in length, have completely inhibited the flowering phase of development of this plant. The shorter 7-hour daily exposures to light under controlled conditions have produced identical results. Thus it appears that the normal flowering period of *Mikania scandens* even in the warmer portions of its range should not occur much later in the season than the period when the days are not less than 12 hours in length. This seems to be the case in Florida, where the blooming season of Mikania is confined to August and September, as it is in much more northern portions of its range. Plants of this type, attaining their best development under daylight lengths of approximately 12 hours, should also find a more or less congenial environment under truly tropical conditions where the days are never much less than 12 hours in length. It is probable that in the Tropics, however, many plants of this type would not only become perennial in their aerial portions, but would also have a more or less continuous flowering period.

Since it has been shown that the stature of some plants increases in proportion to the length of the day to which the plants are exposed under experimental conditions, this factor should be expected to have some influence upon the stature of such plants in their normal habitat. In general, exceptional stature would be attained in those regions in which a long day period allowed the plants to attain their maximum vegetative expression before the shorter days intervened to initiate the reproductive period. This condition should hold true not only for different latitudes where a plant has an extensive northward and southward range but for different sowings in the same locality at successively later dates during the season. It is a matter of common observation that the rankest growing individuals among such weeds as the ragweed, pigweed (Amaranthus), lamb's quarters (Chenopodium), cocklebur (Xanthium), beggarticks (Bidens), other conditions being equal, are those which germinated earliest in the season, and consequently were afforded the longest favorable period of vegetative activity preceding the final flowering period. It is also a matter of common observation that all these weeds, when germinating very late in the summer and coming at once under the influence of the stimulus of the shortening days, blossom when very small, often at a height of only a few inches.

Many species of plants have an extensive northward and southward distribution. In these instances it may be that such species are capable of reacting successfully to a wide range of different lengths of day, or it is possible that the apparent adjustment to such a wide range of conditions may depend upon slightly different physiological requirements of different types which have been developed as a result of natural selections. It yet

remains to be seen whether those individuals of a given species which grow successfully in high latitudes have the same physiological requirements with respect to length of day as those growing quite as successfully near the equator. In any study of the behavior of plants introduced from other regions, with a view to determining certain economic qualities, it is evident that the factor of length of day must be taken into consideration as a matter likely to have great significance.

## LENGTH OF DAY AS A FACTOR IN CROP YIELDS

From the facts which have been developed in this paper it would seem that the seasonal change in length of day is a hitherto unrecognized factor of the environment which must be taken into account when dealing with the problems in crop production. So far as is now known, the length of the day is the most potent factor in determining the relative proportions between the vegetative and the fruiting parts of many crop plants; and, in fact, as already pointed out, fruiting may be completely suppressed by a length of day either too long or too short. In some crop plants the vegetative parts alone are chiefly sought, while in others the fruit or seed only are wanted, and in still others maximum yields of both vegetative and reproductive parts are desired. It is apparent that the merits of different varieties or strains may depend largely on the relative length of day in which they are grown, and, therefore, the date of planting may easily become the decisive factor. These are matters of vital importance to the plant breeder and the agronomist. Obviously, a delay of even two or three weeks in seeding certain crops because of inclement weather conditions or other considerations may bring about misleading results. It is to be remembered, furthermore, that planting too early may be equally inadvisable, for crops requiring relatively short days for blossoming may thus come under the influence of short days in early spring, resulting in "premature" flowering and a restricted amount of growth. An impressive lesson as to the influence of length of day on the size attained by the plant before blossoming is seen in the relative heights of consecutive plantings of the Biloxi soybean, as shown in figure 3. For maximum yields of many crops it is essential that the date of planting be so regulated as to insure exposure of the plant to the proper length of day, due regard being had for the specific light requirements of each crop as well as for the relative values of the vegetative and fruiting portions of the plant.

## RESULTS OBTAINED WITH ARTIFICIAL LIGHT USED TO INCREASE THE LENGTH OF THE DAILY ILLUMINATION PERIOD DURING THE SHORT DAYS OF WINTER

These results are of particular significance, since increasing the duration of the illumination period of the short winter day by the use of electric light of comparatively low intensity has consistently resulted in

initiating or inhibiting the reproductive or the vegetative phases of development, depending upon whether the plants employed normally require long or short days for these forms of expression. In these experiments a greenhouse 50 feet long, 20 feet wide, and 12 feet high to the ridge, with side walls of concrete 5 feet high to the eaves, was provided with 34 tungsten filament incandescent lights, each rated at 32 candlepower, evenly distributed beneath the glass roof. As a control, a similar greenhouse without artificial light was used. The long axis of these houses was on a north and south line. The temperature was approximately the same in the two greenhouses, ranging at night around 60° to 65° F. and 75° to 80° during the day. The unlighted greenhouse, however, tended to run two to three degrees higher than the illuminated house. Beginning on November 1 the electric lights were switched on at 4.30 p. m. and turned off at 12.30 a. m., this procedure being followed throughout the course of the experiments. Supplementing the natural length of the winter days with this 8-hour period of artificial illumination has given about 18 hours of continuous daily illumination, approaching in length the summer days of southern Alaska. Under these conditions the following results have been obtained:

A large clump of *Iris florentina* L., with all earth intact, was transplanted October 20, 1919, to each of the two greenhouses. The plants exposed to the long daily period of illumination began growing vigorously at once, soon attaining the normal size for this species, and produced blossoms on December 24 and December 30. The controls remained practically dormant and showed no tendency to blossom as late as February 12, 1920.

Seed of spinach (*Spinacea oleracea* L.), Bloomsdale Curley Savoy,[1] was sowed November 1, 1919, and came up in both houses on November 6. The plants in the control house, 20 to 25 in number, grew very slowly, producing low, compact, leafy growths or rosettes, and gave no evidence of blossoming as late as February 12. The plants in the lighted house elongated very rapidly, soon developing flower stalks, and all blossomed in the period between the dates December 8 and December 23. These have continued to elongate more or less, blossoming and shedding pollen continuously, thus becoming in effect "everblooming" plants.

Seed of cosmos (*Cosmos bipinnata* Cav.) was sowed November 1, 1919, and germinated in both houses November 5. In each greenhouse 40 to 45 plants were grown. The plants in the control house quickly flowered, and all blossomed in the period from December 22 to January 2. The plants in the lighted house grew well but remained in the strictly vegetative stage and were showing no indications of blossoming on February 12. On this date the control plants averaged 30 inches in height and the plants in the lighted house 60 inches.

[1] Horticultural variety.

Seed of radish (*Raphanus sativus* L.), Scarlet Globe,[1] was sowep November 1, 1919, coming up in both lighted and unlighted houses November 5. On February 12 the control plants, although more stocky and having larger roots, showed no indications of developing flower stems. In the lighted house, however, the plants had developed smaller roots, and flower buds were plainly in evidence, showing that the plants would soon blossom, as is their normal behavior in response to the long summer days out of doors.

Seedlings of the Maryland Mammoth variety of tobacco were transplanted to 12-quart iron pails on November 10, on which date they were placed in the control and the lighted houses. The control plants, six in number, exhibited the typical behavior of winter-grown Maryland Mammoth plants, all blossoming during the period from December 31 to January 8. The plants in the lighted house, six in number, behaved as typical summer-grown mammoths, becoming very compact, stout and leafy, with no indications of blossoming on February 12. On this date these plants had already produced many more leaves than the control plants.

Bulbs of *Freesia refracta* Klatt were placed in soil in 5-inch pots on July 11, 1919. Four pots of these plants were kept in the large dark house previously described from 4 p. m. to 9 a. m. daily from July 23 till November 15, when they were transferred to the greenhouses, two pots being placed in the control house and two in the lighted house. None of these plants when taken from the dark house on November 15 showed any indications of blossoming. Both lots began blossoming about December 27. In the control house, however, the plants produced many flower stalks and continued to blossom profusely for a long period. The plants in the lighted house, on the contrary, produced but few flower stalks and few blossoms and soon ceased blooming entirely.

Large, robust clumps of wild violets, of the species *Viola papilionacea* Pursh, were transplanted to pots and boxes and placed in the control and lighted houses on October 31, 1919. At the time these plants were removed from the field the abnormally warm autumn weather had forced them into bloom, and many purple, petaliferous blossoms were in evidence. As the winter days continued to shorten naturally in the control house, blossoming was suppressed and no new leaves were produced. These control plants appeared to be almost dormant, except for the production of numerous short, thickened stems which were crowded close to the ground among the old leaves. In the lighted house the production of the purple, petaliferous blossoms also ceased, but vegetative growth was initiated and new leaves appeared in great abundance. Coincident with this marked vegetative activity, the plants continuously produced fertile, cleistogamous flowers in great abundance. This furnishes another example of ever-blooming in response to a favorable length of day. In all respects this behavior of the violets in the lighted house

[1] Horticultural variety.

simulates the normal behavior of these plants out of doors under the influence of the long summer days.

Through the kindness of Dr. D. N. Shoemaker, several varieties of Lima beans (*Phaseolus lunatus* L.), F. S. P. I. No. 46153, from Chincha, Peru, and F. S. P. I. No. 46339, from Guayaquil, Ecuador, were transplanted from the field to the greenhouse. Several plants of each of these varieties were transplanted into each house on October 18, 1919. Up to that time the plants had not flowered but gave evidence in the field of being extremely late varieties in this latitude. The control plants grew rather slowly but soon became markedly floriferous, setting pods freely. On the other hand, the plants in the artificially illuminated house produced an exceptionally rank growth of vines but did not flower.

Biloxi, Tokyo, Peking, and Mandarin varieties of soybeans were sowed November 1, 1919, and came up November 10 in both houses. In the control house the first blossoms appeared on the Biloxi and Mandarin about December 24, and on the Tokyo and Peking about December 18. In the artificially lighted house the early variety, Mandarin, blossomed on about the same date as in the control house; but under the longer light exposure the plants continued to grow vigorously, and only a very few blossoms appeared, suggesting a tendency toward gigantism. The few blossoms which formed, however, were normal and developed normal pods, while those on the control plants were cleistogamous and sterile. As late as February 12 the other three varieties showed no indications of blossoming. On that date all varieties were much taller in the electrically lighted house than in the control house.

Seed of Beggar-ticks (*Bidens frondosa* L.) were sowed in both houses on November 19, 1919, and came up in each on December 1. When the plants were very small they were transferred from the flats to 5-inch pots. The transplanting took place on December 19, and on January 12 all the control plants in the unlighted house, 8 or 10 in number, were showing tiny flower heads, although these had attained a height of only 1 to 2 inches. These flower heads came into expression as soon as the plants had developed the second pair of foliage leaves above the cotyledons. The plants in the lighted house continued to produce vegetative growth and gave no evidence of producing flower heads as late as February 12. Two of these plants which had attained a height of 8 to 9 inches in response to the lengthened period of illumination in the artificially lighted house were transferred to the control house on December 19. On January 12 both plants had produced flower heads in response to the naturally short winter days prevailing in this house and gave promise of blossoming in a short time. The sister plants remaining in the illuminated house continued to produce vegetative growth, with no evidence of blossoming.

Buckwheat (*Fagopyrum vulgare* Hill) was sowed November 1, 1919, and came up in both houses on November 7. In the control house 28

plants were grown, and 32 plants were grown in the illuminated house. The dates on which the first blossoms appeared on the control plants exposed to the short winter days extended over a range of only about a week—from December 4 to December 10, inclusive. On the other hand, the dates on which first blossoms appeared on the plants exposed to the artificially lengthened day extended over a period of about four weeks—from December 6 to January 2, inclusive. On February 12 the control plants averaged uniformly only 24 inches in height and had practically ceased growing and blooming. The plants in the artificially illuminated house, on the contrary, continued to grow vigorously and to flower freely, having attained an average height of 58 inches, some of the taller being more than 9 feet in height on February 12. These taller plants blossomed much later than the others and produced very few blossoms, thus showing a tendency to become giant forms in response to the artificially produced longer day. The ever-blooming tendency of the plants as a whole, however, was much more marked under the influence of the lengthened illumination period than in the control greenhouse. Again, although the control plants showed very uniform behavior in the range of their earliest blossoming, it is evident that the artificially lengthened period of illumination has in some manner led to a greatly extended range in the time of blossoming. Whether this really represents an unequal response of several more or less distinct, intermingled races to the artificially increased length of day or may be due in part to a more profound physiological variability which has been induced can not be determined until systematic selection and breeding studies have been carried on.

It will be evident that these data dealing with an artificially lengthened illumination period obtained by means of the electric light greatly strengthen the results of the experiments secured during the previous summer by artificially shortening the natural period of illumination through the use of dark houses. The results with the Maryland Mammoth variety of tobacco, the several soybean varieties in question, and the radish are of special significance since they were obtained by methods the direct converse of those used during the summer. Although the intensity of the electric light was undoubtedly far below that of normal sunlight, it was sufficient to initiate or to suppress the reproductive and vegetative activities of these three species as did the long days of the summer time. With respect to the ever-blooming behavior of certain of the plants under study, the results obtained indicate that this behavior is likely to follow when an approximately constant daily illumination period of a duration favorable to both growth and reproduction is maintained for a sufficient length of time. It thus seems possible that the comparatively uniform length of day prevailing in the Tropics accounts for the particular abundance of ever-bloomers in that region.

## IS THE RESPONSE TO DIFFERENCES IN THE LENGTH OF DAY A PRINCIPLE OF GENERAL APPLICABILITY IN BIOLOGY?

Experience has abundantly demonstrated the fact that the biologist who attempts to draw sweeping generalizations regarding responses of plants or animals as a whole to conditions of the environment is in serious danger of going astray, even though his observations be based on the behavior of relatively large numbers of species. With this fact clearly in mind, the following suggestions are put forward tentatively but as possibly being of sufficient interest to justify careful consideration on the part of biologists especially concerned in the fields touched upon. It has been clearly brought out in this paper that for a number of plant species the appropriate length of day acts, not merely as an accelerative, but rather as an initiative influence in bringing into expression the plant's potential capacity for sexual reproduction. Perhaps, as an equally satisfactory way of expressing the fact, it may be said that the length of the day exercises a truly determinative influence on plant growth as between the purely vegetative and the (sexually) reproductive forms of development. The response to length of day may be expected to hold for other species, although it would be premature at present to assert that all higher plants will be found to respond to this factor.

One is naturally inclined to inquire whether, also, the length of day is a controlling factor in sexual reproduction among the lower forms of plant life. The observed behavior of some of these lower forms certainly suggests that they come under the influence of the seasonal range in length of day. A single instance will suffice to illustrate the parallelism existing between the vegetative and the reproductive periods of activity, on the one hand, and the periodical change in the length of the day, on the other. Reference is made to the work of Lewis (*14*), in which it is shown that in certain species of red Algae there is a definite seasonal periodicity in the appearance of sexual and asexual forms. In brief, the July growth of these species consists primarily of tetrasporic or asexual individuals, while through August the growth is characterized by a predominance of sexual plants produced from the tetraspores of the July crop of plants. The carpospores of autumn become sporelings which persist through the winter and give rise to the tetrasporic plants of the early summer period. Should it be true that lower plants respond to differences in length of day as do some of the higher species it may be expected that various relationships between annual and perennial forms, differences in sensibility to relatively long and short days, and other facts which have been shown to apply to these higher species would likewise hold true for lower organisms. It is possible, even, that the seasonal activities of some of the parasitic microorganisms are the result of response to changes in day length.

As to animal life nothing definite can be said, but it may be found eventually that the animal organism is capable of responding to the

stimulus of certain day lengths. It has occurred to the writers that possibly the migration of birds furnishes an interesting illustration of this response. Direct response to a stimulus of this character would seem to be more nearly in line with modern teachings of biology than are theories which make it necessary to assume the operation of instinct or volition in some form as explaining the phenomena in question.

## CONCLUSION

The results of the experiments which have been presented in this paper seem to make it plain that of the various factors of the environment which affect plant life the length of the day is unique in its action on sexual reproduction. Except under such extreme ranges as would be totally destructive or at least highly injurious to the general well-being of the plant, the result of differences in temperature, water supply, and light intensity, so far as concerns sexual reproduction, appears to be, at most, merely an accelerating or a retarding effect, as the case may be, while the seasonal length of day may induce definite expression, initiating the reproductive processes or inhibiting them, depending on whether this length of day happens to be favorable or unfavorable to the particular species. In broad terms, this action of the length of day may be tentatively formulated in the following principle: Sexual reproduction can be attained by the plant only when it is exposed to a specifically favorable length of day (the requirements in this particular varying widely with the species and variety), and exposure to a length of day unfavorable to reproduction but favorable to growth tends to produce gigantism or indefinite continuation of vegetative development, while exposure to a length of day favorable alike to sexual reproduction and to vegetative development extends the period of sexual reproduction and tends to induce the "ever-bearing" type of fruiting.

The term *photoperiod* is suggested to designate the favorable length of day for each organism, and *photoperiodism* is suggested to designate the response of organism to the relative length of day and night.

## SUMMARY

(1) The relative length of the day is a factor of the first importance in the growth and development of plants, particularly with respect to sexual reproduction.

(2) In a number of species studied it has been found that normally the plant can attain the flowering and fruiting stages only when the length of day falls within certain limits, and, consequently, these stages of development ordinarily are reached only during certain seasons of the year. In this particular, some species and varieties respond to relatively long days, while others respond to short days, and still others are capable of responding to all lengths of the day which prevail in the latitude of Washington where the tests were made.

(3) In the absence of the favorable length of day for bringing into expression the reproductive processes in certain species, vegetative development may continue more or less indefinitely, thus leading to the phenomenon of gigantism. On the other hand, under the influence of a suitable length of day, precocious flowering and fruiting may be induced. Thus, certain varieties or species may act as early- or late maturing, depending simply on the length of day to which they happen to be exposed.

(4) Several species, when exposed to a length of day distinctly favorable to both growth and sexual reproduction, have shown a tendency to assume the "ever-blooming" or "ever-bearing" type of development—that is, the two processes of growth and reproduction have tended to proceed hand in hand for an indefinite period.

(5) The relationships existing between annuals, biennials, and perennials, as such, are dependent in large measure on responses to the prevailing seasonal range in length of day. In many species the annual cycle of events is governed primarily by the seasonal change in length of day, and the retarding or more or less injurious and destructive effects of winter temperatures are largely incidental rather than fundamental. Hence, by artificial regulation of the length of the daily exposure to light it has been found that in certain species the normal yearly cycle of the plant's activities can be greatly shortened in point of time, or, on the other hand, it may be lengthened almost indefinitely. In certain cases, annuals may complete two cycles of alternate vegetative and reproductive activity in a single season under the influence of a suitable length of the daily exposure to light. Similarly, under certain light exposures some annuals behave like nonflowering perennials.

(6) In all species thus far studied the rate of growth is directly proportional to the length of the daily exposure to light.

(7) Although the length of the daily exposure to light may exert a controlling influence on the attainment of the reproductive stage, experiments reported in this paper indicate that light intensity, within the range from full normal sunlight to a third or a fourth of the normal, and even much less, is not a factor of importance. It follows that the total quantity of solar radiation received by the plant daily during the summer season, within the range above indicated, is of little importance directly so far as concerns the attainment of the flowering stage.

(8) In extensive tests with soybeans, variations in the water supply ranging from optimum to a condition of drought sufficient to induce temporary wilting daily and to cause severe stunting of the plants were entirely without effect on the date of flowering, although in some cases drought seemed to hasten somewhat the final maturation of the seed. Similarly, differences in light intensity, in combination with differences in water supply, failed to change the date of flowering in soybeans.

(9) The seasonal range in the length of the day is an important factor in the natural distribution of plants.

(10) The interrelationships between the length of day and the prevailing temperatures of the winter season largely control successful reproduction in many species and their ability to survive in given regions.

(11) The relation between the length of the day and the time of flowering becomes of great importance in crop yields in many instances and in such cases brings to the forefront the necessity for seeding at the proper time.

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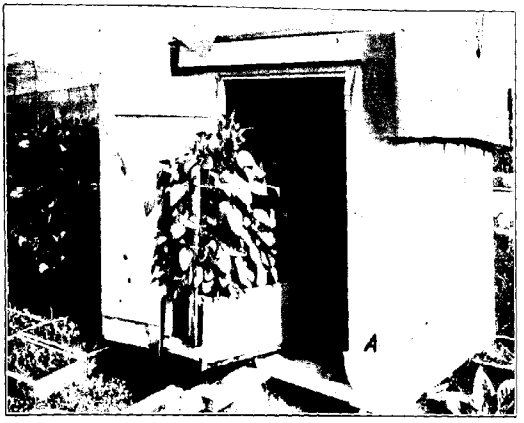
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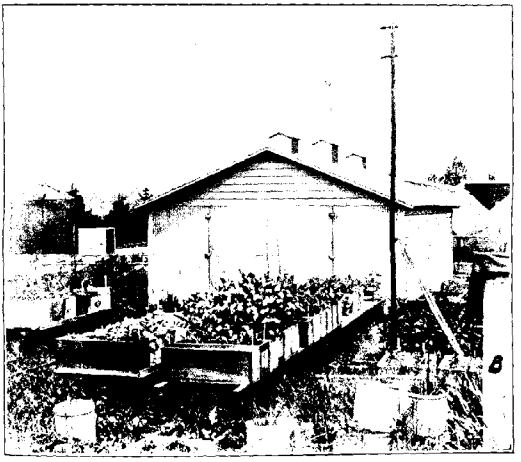
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PLATE 64

A.—Small dark chamber used in the 1918 experiments.

B.—Larger dark house used in the 1919 tests. Trucks and steel tracks used in moving the test plants into and out of the dark house.


A


B


A

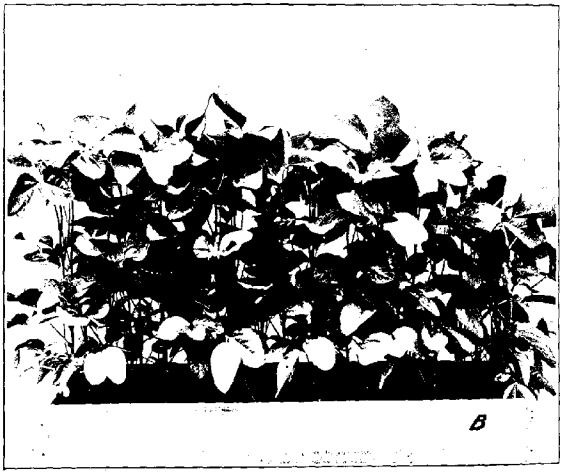

B

PLATE 65

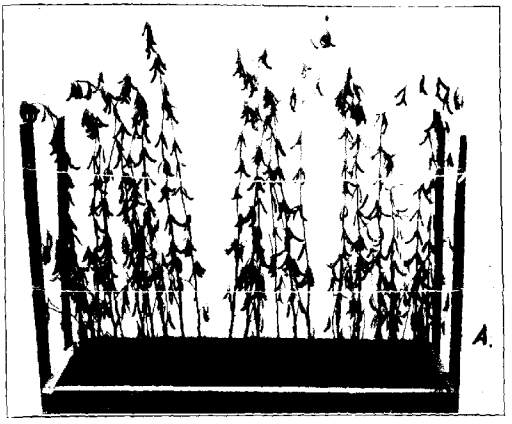
A.—Peking soybeans exposed to the light for 7 hours daily. Note the abundance of full-sized green seed pods. Photographed July 9, 1919.

B.—Control planting of Peking soybeans exposed to the light for the whole day—that is, kept out of doors day and night. No blossoms had appeared when photographed July 9.

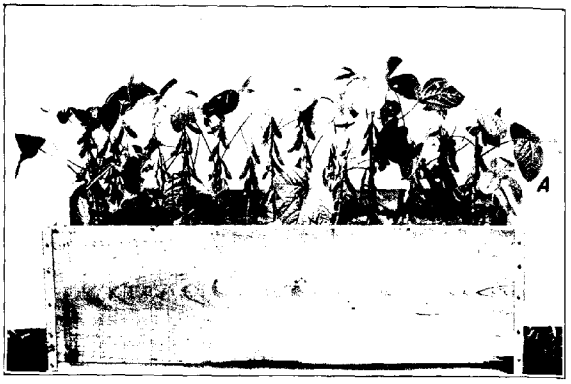
PLATE 66

A.—Peking soybeans exposed to the light for 7½ hours daily, beginning with the blossoming period. When photographed September 13, 1919, the seed pods had fully matured and were ready for harvest.

B.—Control planting of Peking soybeans kept out of doors throughout the test. When photographed September 13 the seed pods were still green and the foliage was just beginning to yellow slightly.


A.


B


A


B

PLATE 67

A.—Biloxi soybeans exposed to the light for 7 hours daily. When photographed August 15, 1919, all seed pods were mature and dry and the leaves were falling.

B.—Control planting of Biloxi soybeans kept out of doors during the test. When photographed August 15 there were no indications of blossoming.

PLATE 68

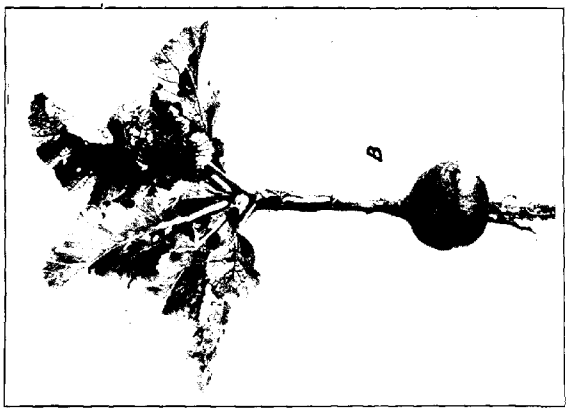
Biloxi soybeans:

A.—Plants in box on left exposed to the light for 5 hours daily. Those in box on right kept out of doors throughout the experiment. When photographed August 15, 1919, the plants on left contained fully matured seed pods and leaves were yellowing, while plants on right had not blossomed.

B.—Plants in box on left exposed to light daily for 7 hours; those on right exposed 12 hours daily. While both lots blossomed and fruited promptly, the plants under the longer light exposure grew much larger than those under the shorter exposure. Photographed August 19.


A


B


B

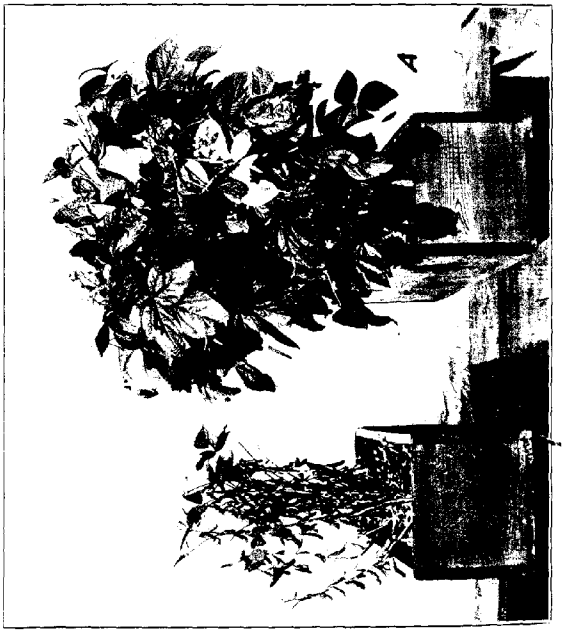

A

PLATE 69

A.— Biloxi soybeans. Plants in box on right exposed to light from daylight to 10 a. m. and from 2 p. m. to dark, a total of 9 to 10 hours daily. Plants in box on left exposed to light from 6 a. m. to 6 p. m., or 12 hours daily. Note marked difference in effectiveness of the two exposures in hastening fruiting and maturation. Photographed September 8, 1919.

B. Radish plant in which the seed stalk was transformed into a vegetative shoot through the influence of the decreasing length of day. Photographed October 12.

## PLATE 70

A.—Maryland Mammoth tobacco in 8-inch pots exposed to light from 9 a. m. to 4 p. m. daily. Seed pods full-grown when photographed August 15, 1919.

B.—Control series of Maryland Mammoth plants kept out of doors. No signs of flowering when photographed August 15.


A


B


A


B

PLATE 71

A.—Maryland Mammoth tobacco in 12-quart buckets exposed to light from 6 a. m. to 6 p. m., or 12 hours daily. Flower heads forming but no open blossoms present when photographed August 19, 1919.

B.—Maryland Mammoth tobacco in 12-quart buckets exposed to light from 9 a. m. to 4 p. m., or 7 hours daily. Seed pods formed when photographed August 19.

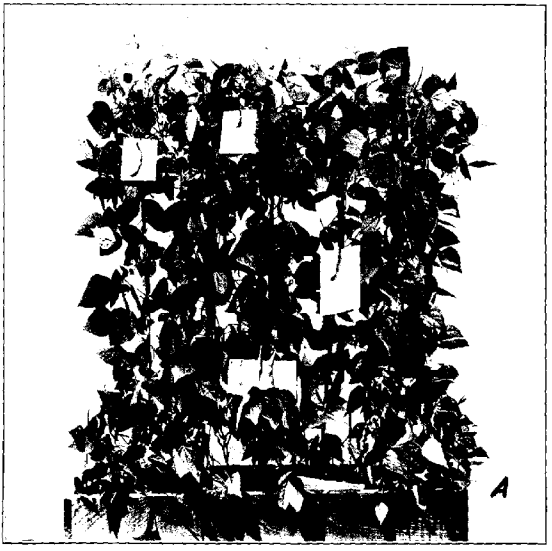
## PLATE 72

A.—Control series of Maryland Mammoth tobacco in 12-quart buckets left out of doors during the experiment. Flower heads just beginning to show when photographed August 19, 1919.

B.—*Aster linariifolius* L. Plants in box on left exposed to light from 9 a. m. to 4 p. m. daily. In full bloom when photographed June 24. Plants in box on right left out of doors during the test. Showed no indications of flower heads when photographed June 24.


A


B


A


B

## PLATE 73

A.—*Phaseolus vulgaris* from Peru and Bolivia exposed to light from 9 a. m. to 4 p. m. Contained full-grown seed pods when photographed August 15, 1919.

B.—Control series of Phaseolus left out of doors during the experiment. Showed no indications of flowering when photographed August 15.

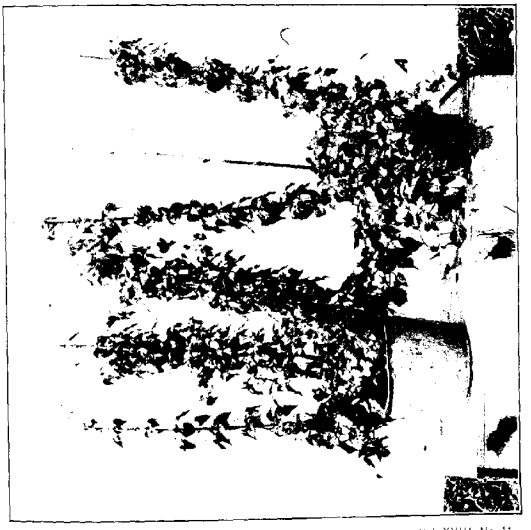
160115°—20—— 5

## PLATE 74

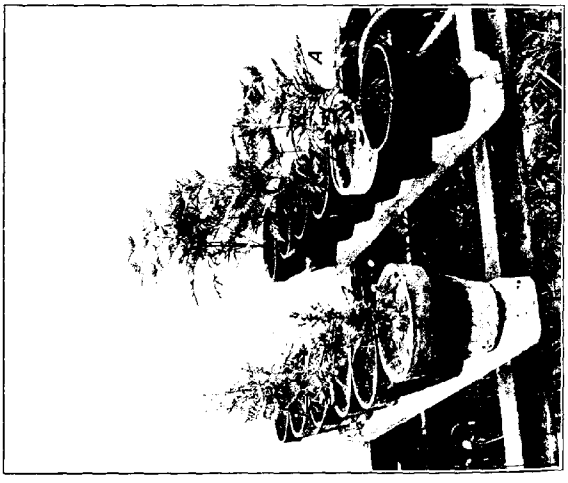
A.—*Mikania scandens* L. exposed to light from 9 a. m. to 4 p. m. daily. Showed no indications of flowering when photographed August 15, 1919.

B.—Control plants of Mikania left out of doors during the test. Blossoming profusely when photographed August 15.


B


C


B


A

## PLATE 75

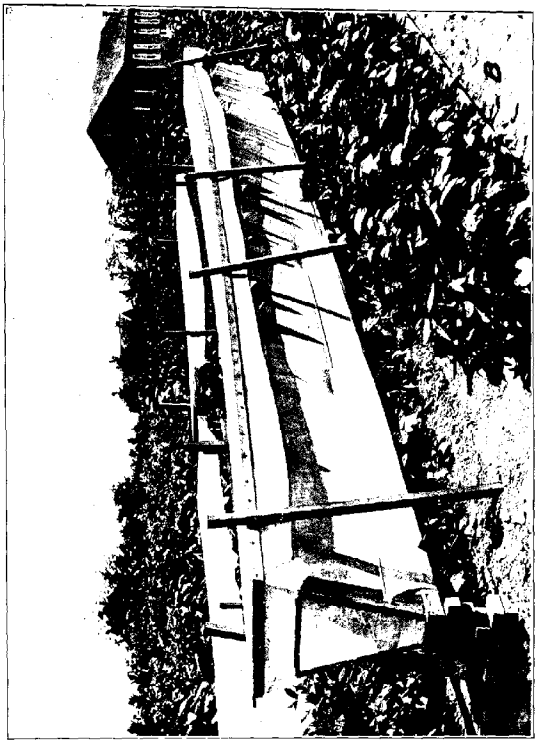
A.—Ragweed. Plants on left exposed to light from 9 a. m. to 4 p. m. daily. Pollen shedding freely from the staminate spikes when photographed July 9, 1919. Plants on right left out of doors as controls. Showed no signs of flowering when photographed.

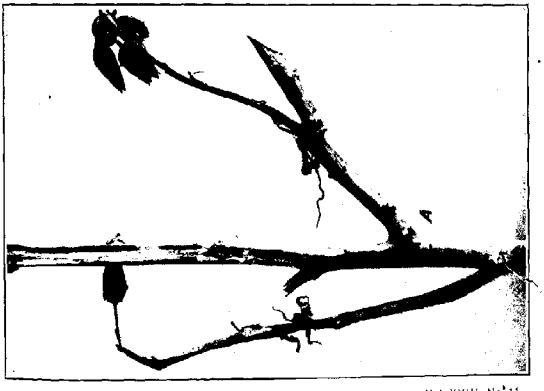
B.—Radish. Plants in box on left exposed to light from 9 a. m. to 4 p. m. daily. No indications of seed stalks when photographed August 19. Plants in box on right left out of doors during the test. Bore an abundance of full-grown seed pods when photographed.

PLATE 76

A.—Portion of stem of Maryland Mammoth tobacco plant, showing the sharp delimitation of dying back of the original growth as controlled by the appearance of new shoots.

B.—Triangular type of shade with cheesecloth covering, used in the 1916 test with soybeans.





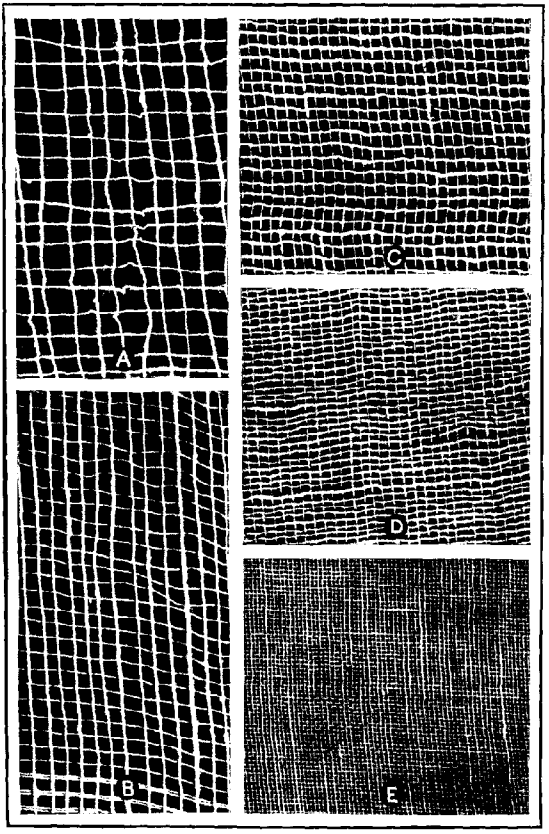

A
B
C
D
E

PLATE 77

A.—Shade cloth, 6 by 6 mesh. Natural size.
B. Shade cloth, 8 by 10 mesh. Natural size.
C.—Shade cloth, 12 by 12 mesh. Natural size.
D.—Shade cloth, 12 by 20 mesh. Natural size.
E.—Standard cheesecloth used in 1916 experiments. Natural size.

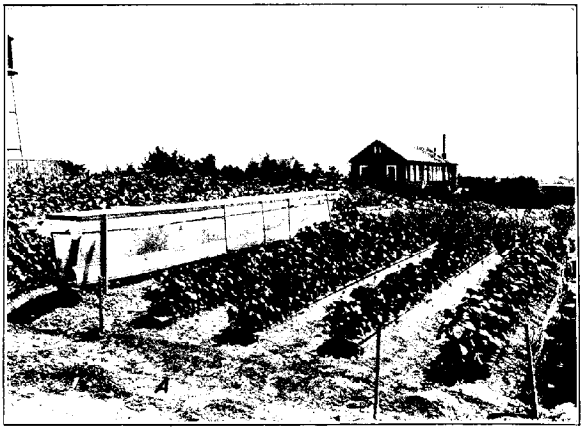
## PLATE 78

A.—Soybeans growing in box set in soil (covers removed), shaded with 12 by 12 mesh netting. Soil kept relatively wet from germination to maturity.

B.—Series of consecutive plantings of soybeans in the field during the summer. All planting shad flowered when photographed September 8, 1919. Note (from left to right) the rapid decrease in height of plants at the time of flowering as the dates of plantings become later and later.


A


B


A


B

PLATE 79

A.—Soybeans growing in four boxes set in the soil and provided with removable covers. To each box different measured quantities of water were added. In addition to the Peking seen in the farther halves of the boxes, an earlier variety, known as Little Brown, was grown in each box.

B.—Carrots. Plants in box on left exposed to light from 9 a. m. to 4 p. m. daily. Had made but little growth of top or root when photographed August 19, 1919. Plants in box on right left out of doors as controls. Had produced much larger tops and roots when photographed.

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